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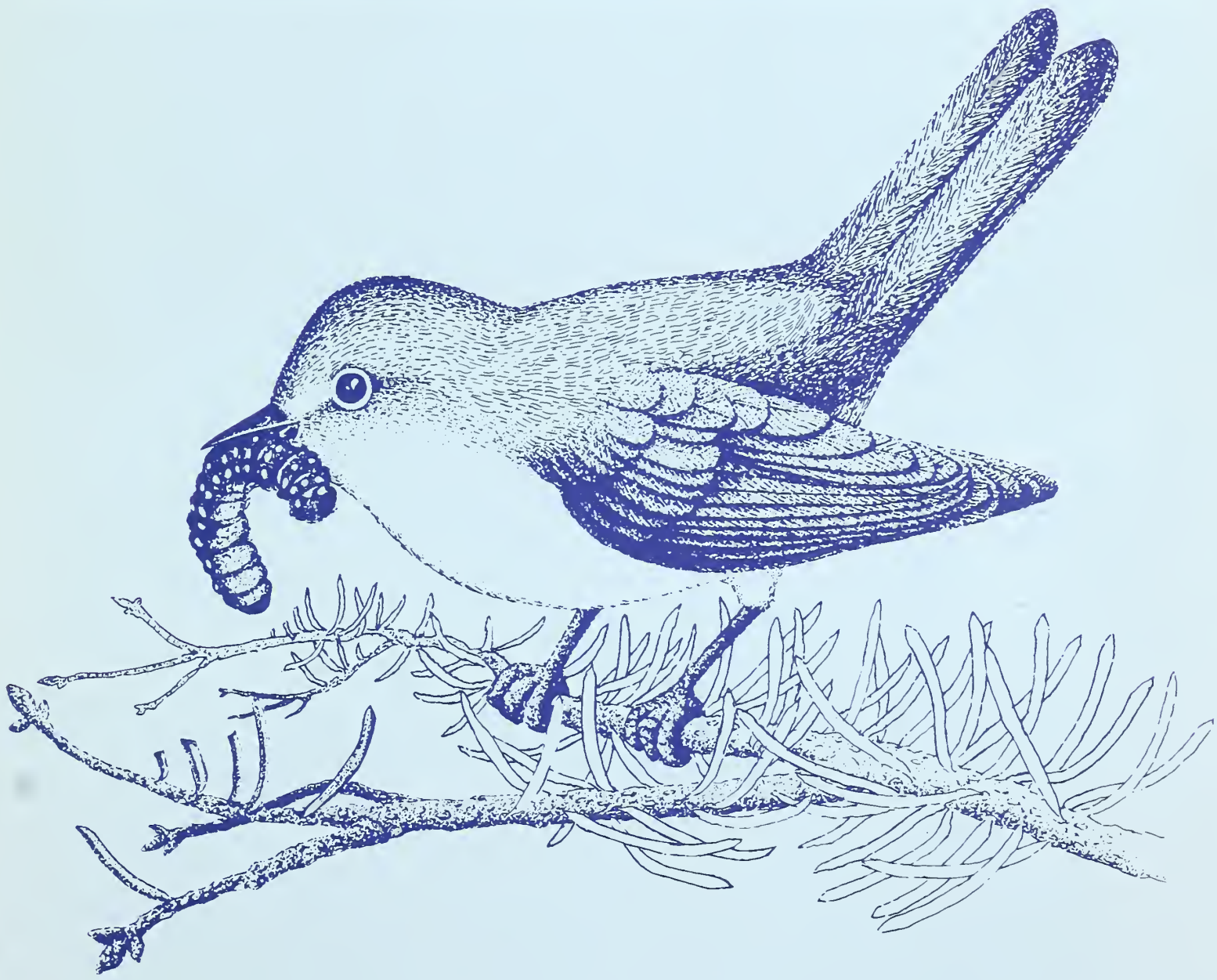
Canada  
United States  
Spruce Budworms  
Program

Prepared by  
Forest Service  
U.S. Dept. of Agriculture  
Washington, D.C.

Bibliographies and  
Literature of  
Agriculture No. 23

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## Relationships of Birds and Spruce Budworms—Literature Review and Annotated Bibliography

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# Introduction

The spruce budworm, *Choristoneura fumiferana* (Clem.), and the western spruce budworm, *C. occidentalis* Freeman, are two of the most destructive forest pests in North America. Millions of acres of spruce-fir forests have been affected by the spruce budworm in Eastern Canada and the Northeastern United States. Similarly, the western spruce budworm has ravaged spruce-fir forests in the Pacific Northwest, the Pacific Southwest, and the Rocky Mountains of Western Canada and the Western United States. Chemical control has been attempted for years at great expense. The effects of chemical treatment on the environment have not been selective and may be long lasting. Because the budworms are natural components of spruce-fir forests, we need natural, long-lasting methods of control and management.

Enhancement of natural control is a desirable feature of integrated pest management. In Europe, where forests have long been exposed to human disturbance, natural predators are believed to prevent irruptions of insect populations. Birds are considered an important component of balanced predator-prey systems, and efforts are made to restore variety and abundance of bird populations (Bruns 1960, Franz 1961, and Williamson 1970). Similar efforts to augment and manage bird populations in northeastern and western spruce-fir forests of Canada and the United States are urgently needed.

This bibliography is intended to aid those interested in the relationships of forest birds and spruce budworms. It is not an exhaustive bibliography; we selected references that we have used in our work and those that we think are representative of the topic.

# Bibliography Format

The annotated references are preceded by a narrative summary for each of the four main topics. The annotated references are in alphabetical order by authors. Each annotated reference is followed by a code that indicates the topic or topics that the reference deals with.

The codes are:

**I—Predation and Bird Populations.**

**I-A. Predation—General.**

**I-B. Numerical and functional responses to spruce budworm populations.**

**I-C. Habitat and bird population changes.**

**I-D. Sampling bird populations.**

**II—Determining Consumption of Budworms by Birds.**

**II-A. Structure and function of avian digestive tracts.**

**II-B. Digestion rates.**

**II-C. Identification of remains in digestive tracts.**

**III—Life Histories of Important Predaceous Birds.**

**IV—Predator-Prey Models.**

To aid readers who are interested in a specific subject, we have listed all references in a subject index.

# I—Predation and Bird Populations

## I-A. Predation—General

Buckner (1971) reviewed the role of vertebrates in the forest ecosystem and the impact of vertebrate predation on forest insect populations. He advocated that forest pest control should take an integrated approach that includes the use of small vertebrates. He defined the ideal predator for encouragement as one that has a high feeding capacity, prefers the target insect, selectively feeds upon insects not attacked by other natural control agents, maintains high population densities, responds quickly to other control measures applied simultaneously, and will be unaffected by subsidiary treatments such as pesticides.

Many species of birds consume spruce budworms during budworm outbreaks (Mitchell 1952, Dowden and others 1953, Kennedy 1978). Birds probably cannot control an epidemic population of spruce budworm (Kendeigh 1947, George and Mitchell 1948), but Holmes and others (1979) found that predation by birds on larval Lepidoptera may be greater than previously thought possible. Birds prevent irruptive insect populations and provide a damper to oscillations of insect numbers (Dowden and

others 1948, Dowden and Carolin 1950, Graham 1967, Mattson 1974). Birds generally consume late-instar larvae (Gage 1968) and pupae of the spruce budworm (Mook 1963, Morris 1963). Little information is available on bird predation on budworm moths and eggs.

Estimates of budworm consumption by birds vary greatly. Estimates of daily consumption by several species of birds are shown in table 1.

## I-B. Numerical and Functional Responses to Spruce Budworm Populations

Buckner (1967) stressed the importance of both numerical and functional responses of avian and mammalian predators on forest insect populations. He divided functional responses into basic components (reaction to increasing prey density) and subsidiary components (food preferences and feeding behaviors such as hoarding and "sport" killing). Numerical responses are divided into breeding and behavioral responses. Behavioral numerical responses are often instantaneous and spectacular. They may be very significant at high prey densities. Roving flocks of birds entering the forest and feeding on budworms exemplify a behavioral numerical response (Mattson and others 1968). In such instances, population movements account for a drastic increase in predators.

Table 1.—Daily consumption estimates

Predator species	Prey species	Prey per day	Prey population	Source
Eastern chipping sparrow	Jack pine budworm, <i>Choristoneura pinus</i> Freeman	125 (larvae, pupae moths)	420,000/acre (1.05 million/ha)	Simmons and Sloan (1974)
Olive-backed thrush	Spruce budworm, <i>Choristoneura fumiferana</i> (Clem.)	74 (pupae)	20,000/acre (50,000/ha)	Mook and Marshall (1965)
Slate-colored junco	Black-headed budworm, <i>Acleris variana</i> Fern.	72	1,000–150,000/acre (2,500–375,000/ha)	Gage, Miller, and Mook (1970)
White-throated sparrow	Black-headed budworm, <i>Acleris variana</i> Fern.	31		
Boreal chickadee	Black-headed budworm, <i>Acleris variana</i> Fern.	15		
Kinglet species	Black-headed budworm, <i>Acleris variana</i> Fern.	10		
Warbler species	Black-headed budworm, <i>Acleris variana</i> Fern.	8		
Warblers, vireos, fringillids, chickadees, kinglets, creepers, nuthatches, thrushes, etc.	Spruce budworm, <i>Choristoneura fumiferana</i> (Clem.)	6g/bird/day = 65–100	500,000–1,000,000/acre (1.25–2.5 million/ha)	George and Mitchell (1948)



Kendeigh (1947) reported that Tennessee, Cape May, and bay-breasted warblers increased during a spruce budworm infestation in Ontario (table 2). During endemic budworm populations, Sanders (1970) studied the same area as Kendeigh and found 123 breeding pairs though Kendeigh found 319. The Tennessee, Cape May, bay-breasted, and blackburnian warblers, which are abundant during spruce budworm infestations, were virtually absent during Sanders' study. MacArthur (1958) reported that Cape May and bay-breasted warblers increased during a period of superabundant food while yellow-rumped (myrtle), blackburnian, and black-throated green warblers maintained populations roughly proportional to the volume of foliage in which they normally feed.

Mook (1963) reported that three species of warblers—the Tennessee, blackburnian, and the bay-breasted—demonstrated a direct numerical response to increasing budworm densities. The strongest response was noted for the bay-breasted warbler, which increased from 10 to 120 pairs per 100 acres (40 ha). However, the percentage of predation of the bay-breasted on budworm populations de-

creased gradually when budworm density exceeded two sixth-instar larvae per 10 ft<sup>2</sup> (0.93 m<sup>2</sup>) of foliage.

Shaub (1956) noted a sudden increase in breeding numbers of evening grosbeaks in areas infested with spruce budworm. Blais and Parks (1964) reported concentrations of evening grosbeaks feeding on spruce budworm during an irruption. Later, Blais and Price (1965) concluded that spruce budworm affects the distribution of evening grosbeaks in Eastern North America.

Morris and others (1958) noted increases in the bay-breasted, Tennessee, and blackburnian warblers and decreases in the magnolia, yellow-rumped (myrtle), and black-throated green warblers during budworm infestations. The bay-breasted warbler increased from 10 to 120 breeding pairs per 100 acres (40 ha), the blackburnian warbler from 5 to 45 pairs, and the Tennessee warbler from 0 to 45 pairs. Similar but less pronounced responses were observed for the Swainson's thrush (olive-backed thrush) and the evening grosbeak. The magnolia, yellow-rumped (myrtle), and black-throated green warblers exhibited inverse responses, possibly because of competition with the other species. The overall response showed that bird populations increased from 200 to 355 pairs per 100 acres (40 ha) for the 10-year period.

Table 2.—Bird populations during endemic and epidemic budworm populations

Breeding pairs/100 acres (40 ha)	Location	Budworm status	Source
115 (overmature stand)	Black Sturgeon Lake, Ontario	Endemic (low-population density)	Sanders (1970)
131 (immature stand)	Black Sturgeon Lake, Ontario	Endemic (low-population density)	Sanders (1970)
168 to 210	Green River, New Brunswick	Before budworm outbreak	Cheshire (1954)
333	Green River, New Brunswick	Epidemic (during outbreak)	Cheshire (1954)
425	Northern Maine	Epidemic	Hensley and Cope (1951)
319	Black Sturgeon Lake, Ontario	Epidemic	Kendeigh (1947)
200 to 355 (all spp.)	Green River, New Brunswick	Endemic to epidemic	Morris and others (1958)
300 (adjusted to 250 for those feeding on budworm)	Lake Clear Junction, New Hampshire	Epidemic	George and Mitchell (1948)

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During the same outbreak, Morris and others (1958) also observed a functional response of birds to increasing prey densities. Many species of birds alter their normal feeding habits to take advantage of plentiful food supplies. For example, ground-feeders, cross-bills, and woodpeckers were frequently observed picking budworm larvae from balsam foliage.

Zach and Falls (1975) reported that ovenbirds exhibited a functional response to outbreaks of the spruce budworm. Ovenbirds generally restrict their feeding behavior to the forest floor and vegetation within reach of the ground. Once spruce budworms reached high densities, however, these birds were frequently observed searching branches of infested conifers and feeding on larvae, pupae, and adults. On the basis of smaller, more tightly packed territories and larger first and subsequent clutches, a numerical response was also noted.

### **I-C. Habitat and Bird Population Changes**

Habitat change resulting from timber stand alteration causes bird populations to change. Thus, natural predation can be modified through habitat manipulation. Successive seral stages of vegetation in spruce-fir forests have associated bird communities (Titterington and others 1979, Crawford and Titterington 1979). Species composition and individual abundance of birds change as vegetation responds to different types and intensities of forest cutting. Intensive cutting creates conditions suitable for an association of birds that forage in a relatively open condition. Other associations are related to dense, low brush and bramble patches; regenerating stands; intermediate-size stands; and mature forests that succeed from intensive cutting or are created by lighter cutting.

Naturally occurring habitat changes also affect bird populations. Martin (1960) related bird species to hydric and xeric forest successional stages in northern coniferous and hardwood forests. Tothill (1923) concluded that the more heterogeneous western forests supported bird populations that controlled spruce budworm numbers and prevented severe defoliation. Conversely, homogeneous forests did not support enough avian predators, and spruce budworm populations declined only after budworms had exhausted their food supply. The implications of Tothill's conclusions and the findings of Crawford and Titterington (1979) and Titterington and others (1979) offer a potential forest management strategy for enhancing natural predators of the spruce budworm. Through timber stand modifications habitat diversity can be increased; thus, the stand can support greater and more diverse bird populations.

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### **I-D. Sampling Bird Populations**

Methods to sample bird populations are (1) mark and retally (Leopold 1933, MacArthur and MacArthur 1974); (2) intersection (Graham 1940); (3) intensive plot counts of all nests or singing males (Williams 1936, Robbins 1970); and (4) some variation of transect counts. All methods have advantages and disadvantages; the choice depends upon the objective in censusing populations (Emlen 1971, 1977; Kendeigh 1944). The nesting, breeding bird, and intersection samples are restricted to the breeding season. Mark and retally samples depend on a constant population, so the technique is also limited by season because of the dynamic nature of bird populations. Transect methods may be used in any season but are hampered by problems involving detectability and sample size. Amman and Baldwin (1960) used a variable-width transect to sample woodpeckers. Colquhoun (1940), Colquhoun and Morley (1941), Emlen (1971, 1977), and West and DeWolfe (1974) used transects of variable width which were based on their ability to detect each species of bird. Franzreb (1976) compared the mapping of singing males to values obtained from a variable-width transect. Eberhardt (1968), Gates and others (1968), and Hayne (1949) evaluated line transects for measuring bird populations.



## II—Determining Consumption of Budworms by Birds

Crops, gizzards, and droppings are commonly used for studying food habits of birds (Korschgen 1971). Esophageal samples (gullets) are preferable for some birds, especially ducks (Swanson and Bartonek 1970). However, small passerine birds often have an empty esophagus (Custer and Pitelka 1975), and this necessitates examination of the gizzard. Droppings may be useful for discerning the food habits of some gallinaceous birds, such as grouse, quail, and pheasants. Recognizable insect parts can pass through the alimentary tract and appear in droppings; however, this aspect has not been fully investigated for birds feeding on spruce budworm.

### II-A. Structure and Function of Avian Digestive Tracts

The physiology of avian digestion and the digestive system were reviewed by Ziswiler and Farner (1972). Parts of the digestive system or alimentary tract most commonly examined in food-content studies are esophagus, crop, proventriculus, and gizzard. Both proventriculus and gizzard comprise the stomach of a bird (fig. 1).

The esophagus is a passageway for food and other material from the pharynx to the stomach. In gallinaceous birds, a lateral diverticulum or expansion of the esophagus forms the crop (fig. 2). The crop serves for temporary food storage, and food is passed from the crop to the stomach at infrequent intervals.

The principal function of the proventriculus or glandular stomach is secretion of gastric juices. The proventriculus also serves as a passageway from the esophagus to the muscular stomach or gizzard. Mechanical digestion, acid proteolysis, and storage are all functions of the gizzard.

Most insectivorous birds have no crops. Feeding generally occurs throughout the day, and food passes from the esophagus into the stomach (fig. 1). By contrast, gallinaceous birds have two general feeding periods, morning and evening. Much food (especially grains) may be consumed rapidly and stored in the crop before passing into the stomach for digestion (fig. 2). But small insectivorous birds seldom have food in the esophagus when postmortem examinations are made.

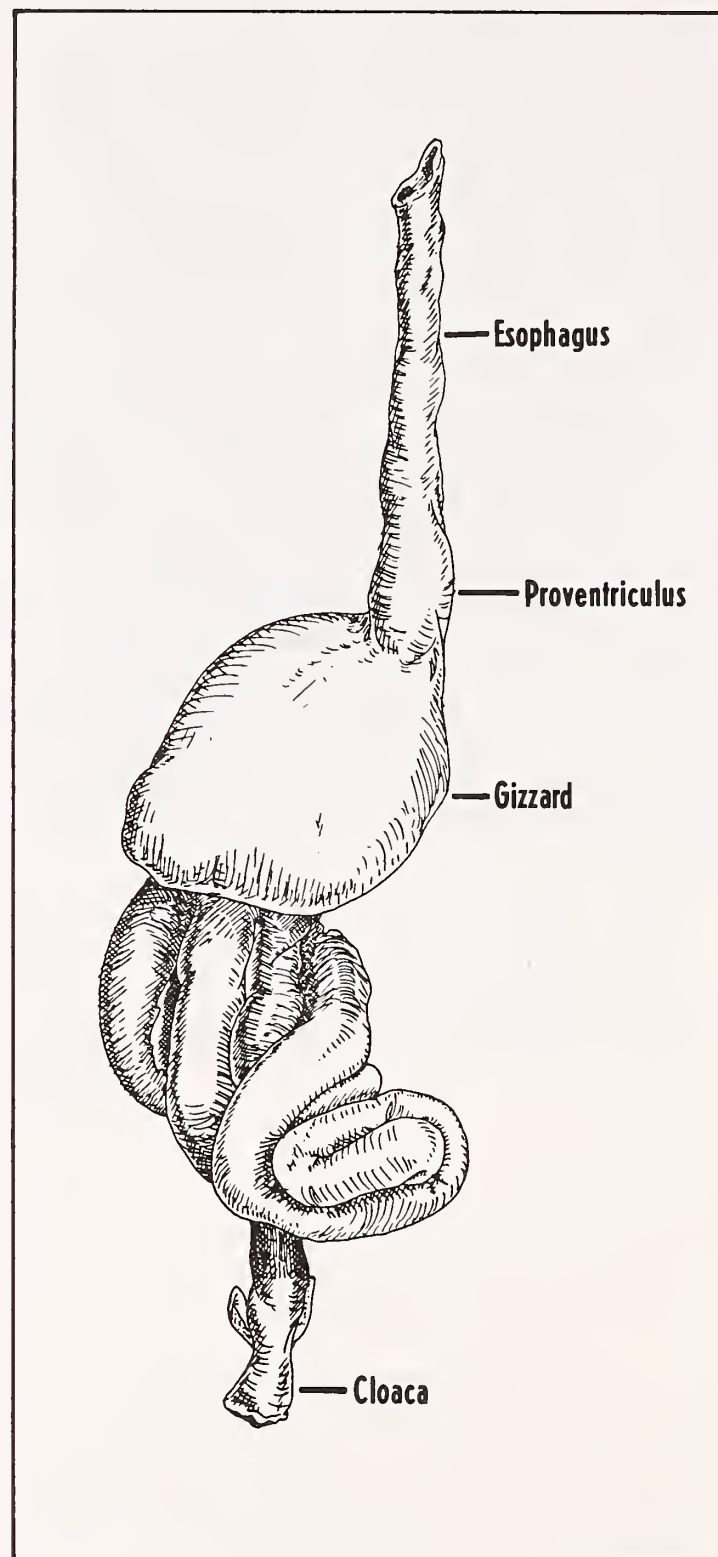


Figure 1.—Digestive tract of insectivorous bird.

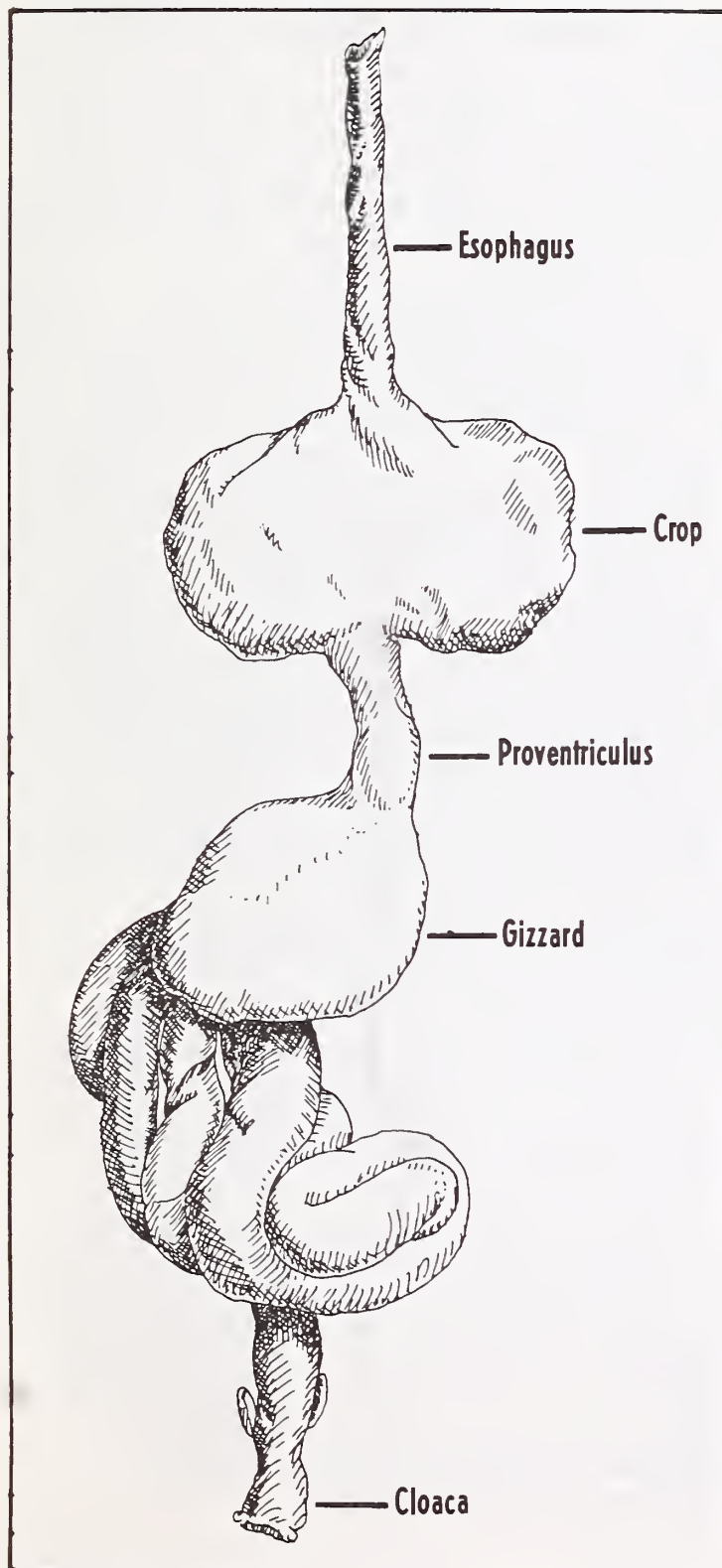


Figure 2.—Digestive tract of gallinaceous bird.

## II-B. Digestion Rates

Digestion rates have been studied in detail for only a few birds and by only a few researchers, for example, Mook and Marshall (1965) and Stevenson (1933). The rates at which foods pass through the alimentary tract vary and are dependent on several factors, including physiological needs or requirements, previous feeding regimes, age of the bird, season, condition of the bird, and the nature of the ingested food itself. Some foods are broken down rapidly and are assimilated more quickly than others. For example, insect larvae, worms, and other soft-bodied invertebrate parts are hardly recognizable after only a few minutes in the gizzard (Custer and Pitelka 1975). Seeds and heavily sclerotized insect parts, on the other hand, are distinguishable for some time after ingestion. Thus, different digestion rates may be encountered for different bird species as well as for different prey food.

Sturkie (1965) lists five methods for investigating the passage of food through the alimentary tracts of birds. The methods are to (1) kill birds at different intervals to observe the location (and condition) of the food in the tract, (2) stain food with dyes so that the food may be identified in feces, (3) recognize foods by their size or shape, (4) observe passage of food with X-rays, and (5) place a cannula or other ligature in the tract.

Because digestion rates vary for different kinds of food, the proportions of some food may be underestimated or overestimated. To compensate for these differences, some investigators have applied correction factors for assessing diet composition (Custer and Pitelka 1975).

Few studies have dealt specifically with the rate at which insects are digested by birds. Fortunately, one such study pertains to the spruce budworm. Mook and Marshall (1965) investigated rates of digestion for spruce budworm larvae and pupae fed to Swainson's thrushes (olive-backed thrushes). Birds were confined for 2 or more hours before being fed spruce budworm and were then killed at various time intervals after ingestion. The investigators found that (1) rates of digestion for larvae and pupae were similar for the first hour; (2) soft parts and sclerotized parts of pupae were digested at different rates; (3) after 90 minutes most soft parts disappeared and only finely fragmented, hard particles remained; (4) cremasters were first removed at a slow rate and then rapidly after 90 minutes; and (5) the gizzard was empty after 2 hours.



Custer and Pitelka (1975) pointed out that digestion is more rapid in starved birds than in well-fed birds. Dillery (1965) concluded that digestion rates of birds vary by groups of prey animals, and that digestion may continue after birds are killed. Injection of a 10-percent formalin solution immediately after collection stops digestion.

Comparison of these findings with other digestion-rate studies demonstrates the variability in different bird species and their food-prey items. In a postmortem examination of a savannah sparrow stomach, Dillery (1965) found parts of adult beetles (but not beetle larvae or harvestmen) 5 minutes after ingestion. He also noted that hard parts, such as mandibles, are similar to gravel and apparently remain in the stomach for some time. Head parts and elytra of carabid beetles were recognizable 35 and 180 minutes, respectively, after ingestion by snow buntings (Custer and Pitelka 1975). Swanson and Bartonek (1970) found that 10 minutes after ingestion 24 percent of dipterous larvae that were fed to blue-winged teal were digested beyond distinction.

Gage and others (1970) used a radioactive tracer to investigate the digestion rates of the bay-breasted warbler, the yellow-rumped (myrtle) warbler, and the white-throated sparrow. The results showed little variation between species, and passage of food through the digestive tract took 2.5 hours. If feeding has been continuous, they estimated that about 35 percent of the food ingested within a 2.5-hour period would still be in the digestive tract at any point in time. Using these data, they converted *apparent* consumption to *real* consumption or the actual number of insects consumed within 2.5 hours. Total consumption per day per acre was then determined for each bird species by (1) the estimated time spent actually feeding and (2) bird densities per acre based on censuses of singing males.

## II-C. Identification of Remains in Digestive Tracts

Identification of food in a bird's stomach often requires special skills and a thorough knowledge of the flora and fauna where samples are collected (Korschgen 1971). For target species identifications, such as for the spruce budworm, the examiner should be thoroughly familiar with budworm morphology.

Most stomach-content identifications are based on finding recognizable insect parts in the esophagus, proventriculus, and gizzard. For the spruce budworm, both hard- and soft-bodied structures of the larva, pupa, and adult are useful for identification. Spruce budworm larvae are seldom found intact in the gizzard except immediately after collection (Mook and Marshall 1965). Hence, identification of budworm larvae in a bird's stomach depends on being able to recognize and distinguish larval parts, including head capsules, thoracic and anal shields, remains of thoracic legs and abdominal prolegs, and other remains. The most definitive parts for identifying individual larvae are remains of the head capsule and mandibles. These parts remain in the gizzard for some time, and right and left members of a mandible pair can be identified to help count larvae consumed. MacKay (1953) describes and illustrates some of the morphological features of spruce and jack pine budworms.

Budworm pupal parts are also distinctive and can be recognized and identified after consumption by birds (Mook and Marshall 1965). The spination on the pupal abdomen and remains of the pupal head, thorax, and wing pads are all aids for identifying budworm pupae. However, the most distinctive part, and one that can be used for distinguishing individuals, is the pupal cremaster. The cremaster of the spruce budworm pupa is a prolongation of the tenth abdominal segment (Jennings and Houseweart 1978). The cremaster is armed with eight strongly hooked setae, and the shape, position, and insertion of these setae differ among lepidopterous species. Although cremasters are relatively small compared with other pupal parts, they are easily recognized and identified. Examiners seeking intact pupae or large pupal remains may overlook cremasters; thus, the importance of budworm pupae in stomach-content studies is diminished.

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Remains of budworm pupae can also be sexed if the eighth and ninth abdominal segments are present (Jennings and Houseweart 1978). Sexing permits determination of possible feeding preferences.

Remains of spruce budworm adults (moths) are commonly seen in postmortem examinations. Adult parts may include wing fragments, fragments of the head and thorax (with associated legs, eyes, and antennae), and abdominal fragments. Definitive identifications usually depend on finding part of the head or parts of the male or female genitalia. Outram (1970, 1971) illustrated both male and female genitalia of spruce budworm. Familiarization with these structures is essential for positive identification of spruce budworm adults.

Identification of small first- and second-instar spruce budworm larvae within a bird's stomach has not been fully evaluated and explored. However, several species—nuthatches, chickadees, creepers, warblers, etc.—glean beneath bark scales, mosses, and lichens, all of which are favored overwintering sites for budworm larvae. The effects of birds feeding on early-instar larvae in late summer, fall, winter, and early spring are not known. Nor do we know the extent of bird predation on egg masses of the spruce budworm. Identification of budworm egg masses in bird gizzards is hampered by the translucent, fragile nature of the egg chorions. Egg size, shape, and pattern of deposition in overlapping rows are clues.

Identification of budworm remains in a bird's stomach also depends on a familiarization with associated lepidopterous species. Associated insects in spruce-fir forests include species of *Acleris*, *Recurvata*, *Dioryctria*, *Zeiraphera*, *Clepsis*, *Archippus*, *Eucordylea*, and *Griselda*. Miller (1950) gives an identification key to some lepidopterous larvae associated with the spruce budworm in New Brunswick. Carolin and Stevens (1979) presented a key for identifying lepidopterous larvae associated with the western spruce budworm, *Choristoneura occidentalis* Freeman, on Douglas-fir and true firs in the Western United States and Canada.



### III—Life Histories of Important Predaceous Birds

The reason that certain bird species become more abundant during spruce budworm outbreaks (numerical response) is explained by the life histories of these birds. MacArthur (1958) compared several life history features of Cape May and bay-breasted warblers with those of blackburnian, black-throated green, and yellow-rumped (myrtle) warblers. He showed that clutch size of the Cape May and bay-breasted warblers was larger than that of the other species, and illustrated with the bay-breasted that clutch size increased during years of spruce budworm abundance. The only other warbler regularly laying large clutches was the Tennessee warbler, which also increased during spruce budworm irruptions. Species that lay large clutches are often subjected to a high rate of nestling mortality because adults cannot effectively feed all the young that hatch. However, MacArthur (1958) noted that adult warblers will feed the young of other warblers of their own and other species. If this feeding is done by non-nesting adults, dense warbler populations during spruce budworm outbreaks may enhance the survival of Cape May, bay-breasted, and Tennessee warbler young.

Nest location, time of hatching, and foraging patterns enable Cape May and bay-breasted warblers to frequent the same stand and not compete for nesting or foraging sites. Cape May warblers customarily feed in the tops of mature trees on the outer tips of the branches, whereas bay-breasted warblers feed in midcrown and along the base of lower branches. These feeding patterns show minimal overlap with the Cape May for feeding sites (MacArthur 1958, Morse 1978). The Cape May nests near the top of mature trees in dense cover near the trunk, whereas the bay-breasted nests away from the trunk, generally closer to the ground (Palmer 1949). The Cape May completes its nest earlier than the bay-breasted (MacArthur 1958) and will be actively feeding young when late-stage spruce budworm larvae are active in outer portions of the upper crown. The bay-breasted begins actively feeding young about a week later, when larval activity has moved

to midcrown and interior portions of the tree. Thus, Cape May and bay-breasted warblers are complementary predators on spruce budworm larvae. The greater food-conditioned fecundity and compatibility of these two "budworm-responders" may explain why other congeneric species decrease when these warblers increase dramatically during spruce budworm infestations. The congeneric blackburnian, black-throated green, and yellow-rumped (myrtle) warblers—although they do not compete severely for feeding sites (Morse 1967a, 1967b, 1968, 1973)—do not have the advantages of (1) bringing off broods at different and propitious times (MacArthur 1958), and (2) being free from nest site competition (Palmer 1949).

In modeling spruce budworm population change, Holling<sup>1</sup> hypothesized that predation by woodpeckers helped maintain spruce budworm populations at endemic levels. A study of the life histories of these birds does little to support this hypothesis, though woodpecker populations have increased after spruce budworm outbreaks (Van Tyne 1926). Woodpecker populations are generally low in spruce-fir types. With the exception of the black-backed three-toed woodpecker, most species are associated with hardwood types (Palmer 1949). Woodpecker populations are generally limited by suitable nesting and roosting sites (Beebe 1974).

<sup>1</sup> Holling, C. S. Spruce budworm workshop; 1976 April 28–30. Orono, Maine: Univ. of Maine; 1976. Unpubl. worksheets.

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Woodpeckers search for food on the trunk and larger limbs near the tree bole; late-stage spruce budworm larvae are found on small branches and branch tips. Thus, one would expect little predatory effect from woodpeckers; but the downy woodpecker feeds from small limbs and branch tips, where it should encounter spruce budworm larvae. Jackson (1970) described four types of feeding by downy woodpeckers. Of these, surface gleaning accounted for a substantial portion of its feeding throughout the year. Generally, the smaller the woodpecker, the smaller the nest tree required (Conner and others 1975). Downy woodpeckers nest in small hardwood or softwood trees, preferably those containing rot, and these trees often are in spruce-fir stands. Downy woodpeckers are resident species and feed periodically throughout the winter, often in the company of black-capped and boreal chickadees and red-breasted nuthatches. Hairy woodpeckers are also active winter feeders. Budworm larvae that overwinter on limbs and in bark crevices may be more available as food for woodpeckers, particularly when the buffering effect of alternate prey species is reduced or eliminated (Morris and others 1958, and Baldwin 1968). The effects of winter predation by woodpeckers on spruce budworm larvae are unknown but could be important in spruce-fir stands where hardwood species occur.

Woodpecker populations respond numerically by immigrating to areas where prey has increased (Koplin 1969, Kilham 1960). Blackford (1955) reported substantial control of overwintering insect populations by concentrated woodpecker numbers in localized areas. Most reports indicated that woodpeckers aggregate during winter when territorial bonds are weakest.

Woodpeckers show certain biotic characteristics in common with the previously mentioned wood warblers that respond to spruce budworm increases. They both have relatively large clutch sizes; woodpeckers may lay three to eight eggs (Bent 1953). Fledgling survival rates are high. Woodpecker young are protected by the nest cavity and parental attention, which extends for several weeks after fledging (Bent 1953).

Many management opportunities exist for encouraging woodpeckers and other hole-nesting birds. In Europe, where birds are acknowledged to be important agents in the prevention of insect epidemics (Beebe 1974), nest boxes are used to supplement natural nest cavities (Bruns 1960, Tinbergen 1960, Williamson 1970). Franz (1961) reported that forest plots provided with nest boxes sustained no outbreaks or a lesser outbreak of forest insects than did control plots with no nest boxes. Conner and others (1975) recommended changes in forest management practices to increase woodpecker populations. The changes were oriented toward providing nest sites. Woodpeckers, unlike wood warblers, are not limited by food; they are limited by nest sites.

## IV—Predator-Prey Models

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Mathematical modeling of predator-prey relationships is pertinent to studies of bird impact on spruce budworm. However, the literature on this specific topic is limited. Thus, most of the following references do not refer specifically to spruce budworm but to modeling of birds or other predaceous species and various prey species. These references should be useful to those interested in modeling bird and spruce budworm populations.

Watt's (1959) article evaluated five classical mathematical models. Royama (1971) compared logical structure of major existing models. He pointed out that the logical structure in models proposed before 1935 (classical) is sound, but the assumptions involved are often inadequate to describe a biological system. Models proposed after 1955 either involve contradiction in logic or are much too often used erroneously. Pyke and others (1977) compared models and stated that the simple models so far formulated are supported reasonably well by data but require much modification. All except five of the references selected for this section were published in 1970's.

The subjects covered are mutual interference (Beddington 1975), limit cycles (DeAngelis 1975, May 1972), functional response and stability (Holling 1965; Holling and Buckingham 1976; Oaten and Murdoch 1975a, 1975b; Rosenweig and MacArthur 1963), predator impact on prey (Koplin 1972), selective predation (Manley and others 1972, Royama 1970), optimization (Marten 1973, Rapport 1971), parasite and predator comparisons (Griffiths and Holling 1969, Rogers 1972), and inconspicuousness (Seierstad and others 1965).



# Annotated Bibliography

Amman, Gene D.; Baldwin, Paul H. A comparison of methods for censusing woodpeckers in spruce-fir forests of Colorado. *Ecology*. 41:699-706; 1960.

On the basis of field operation, completeness of count, and variation in results, compares nine woodpecker census methods in three areas of spruce-fir forest. The variable-width-strip method proved best with moderately large populations of woodpeckers. I-D

Andrewartha, H. G.; Birch, L. C. The distribution and abundance of animals. Chicago, IL: Univ. Chicago Press; 1954. 782 p.

Includes methods of assessing animal populations and general theories to account for changes in natural populations. Density-independent and density-dependent factors are reviewed and found to be largely artificial. Various mathematical models for host-predator relationships are examined and found inadequate to explain many natural occurrences. I-A; IV

Baldwin, P. H. Woodpecker feeding on Engelmann spruce beetle in windthrown trees. USDA For. Serv. Res. Note RM-105. Fort Collins, CO: Rocky Mount. For. and Range Exp. Stn.; 1968. 4 p.

Northern three-toed and hairy woodpeckers fed at windthrown Engelmann spruce trees infested with Engelmann spruce beetle, *Dendroctonus obesus* (Mann.). Sections of the infested boles were covered with screen to prevent woodpecker feeding over the winter and the following summer. Woodpeckers caused 70 to 79 percent brood mortality. Predation on the Engelmann spruce beetle in windthrown trees appears to be important in declining infestations. III

Beals, E. W. Forest bird communities in the Apostle Islands of Wisconsin. *Wilson Bull.* 72:156-181; 1960.

Bird populations within forests of the Apostle Islands in Lake Superior were related to a community gradient. A two-dimensional ordination based on the avifaunal similarities between stands was constructed. Many bird species and vegetational characteristics showed definite patterns within the ordination. III

Beaver, D. L. Feeding niches of flycatchers in a montane forest in Colorado. Fort Collins, CO: Colorado State Univ.; 1967. 122 p. M.S. Thesis.

Spatial segregation of feeding zones and selection of different foods reduced competition between three species of flycatchers during a spruce budworm epidemic. I-C

Beaver, Donald L.; Baldwin, Paul H. Ecological overlap and the problem of competition and sympatry in the western and Hammond's flycatchers. *Condor*. 77:1-13; 1975.

The study shows that the western flycatcher, *Empidonax difficilis*, and Hammond's flycatcher, *Empidonax hammondii*, occupy overlapping territories in aspen-conifer habitats; and Hammond's flycatcher also nested in aspen habitat in the presence of the western wood pewee, *Contopus sordidulus*. Coexistence was accompanied by (1) subdivision of the foraging niche, and (2) subdivision of food resources. Hammond's flycatcher fed significantly higher than the western flycatcher in aspen-conifer habitat, but the size of food items in their diets was not significantly different. Hammond's flycatcher fed in the same vertical zone as the western wood pewee, but the pewee took larger prey. I-A,C

Beddington, J. R. Mutual interference between parasites or predators and its effects on searching efficiency. *J. Anim. Ecol.* 44:331-340; 1975.

Presents a model that shows the variation in searching efficiency. The model is applied to relationships between searching efficiency and parasite density. A physical interpretation shows that the intrinsic capability of a predator to search an area is never realized. IV

Beebe, S. P. Relationships between insectivorous hole-nesting birds and forest management. New Haven, CT: Yale Univ. Sch. For. Environ. Stud.; 1974. 49 p. Unpubl. rep.

Reviews the literature on general relationships between insectivorous hole-nesting birds and forest management. The most important limiting factor on populations of hole-nesting birds is the scarcity of suitable holes. The security of the hole-nest results in relatively high breeding potential and much competition for nest-sites. Excavating woodpeckers play an important role in providing nest-holes for secondary hole-nesters. Artificial nest boxes have been used successfully to increase populations of hole-nesting insectivorous birds in commercial forests. Insectivorous hole-nesting birds play an important role in regulating forest insect populations. Protection of hole-nesting bird populations by promoting diversity, leaving snags, and using other means is advocated. III

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Bent, A. C. Life histories of North American wood warblers; order Passeriformes. U.S. Natl. Mus. Bull. 203. Washington, DC: Smithson. Inst. Press; 1953. 734 p.

Provides data on members of the family Parulidae. Notes by species include a general description, courtship, nesting, young, plumage, food, behavior, voice, field marks, enemies, and fall and winter characteristics. Notes on distribution include range, breeding range, winter range, migration dates, banding results, casual records, and various egg dates. **III**

Blackford, J. L. Woodpecker concentration in burned forest. *Condor*. 57:28-30; 1955.

Describes the attraction of feeding activities of woodpeckers in a fire-damaged Douglas-fir/yellow pine forest of northwestern Montana. Woodpeckers were attracted to fire-damaged and weakened trees infested with wood-boring insects. **III**

Blais, J. R.; Parks, G. H. Interaction of evening grosbeak (*Hesperiphona vespertina*) and spruce budworm (*Choristoneura fumiferana* (Clem.)) in a localized budworm outbreak treated with DDT in Quebec. *Can. J. Zool.* 42:1017-1024; 1964.

Evening grosbeaks are important predators of the spruce budworm. Migrating birds can reduce insect populations at the time of outbreaks, especially when these outbreaks occur in restricted areas. **I-B**

Blais, J. R.; Price, P. W. Further evidence of a relationship between spruce budworm and evening grosbeak populations. *Can. Dep. For. Bimon. Prog. Rep.* 21(3):1; 1965.

A study was made during a spruce budworm outbreak in central New Brunswick to determine the effect of evening grosbeaks on budworm populations. The area had been partially treated with DDT since 1960. The proportion of budworm population destroyed by grosbeaks was not significant since insect numbers continued to be high. **I-B**

Bond, R. R. Ecological distribution of breeding birds in the upland forests of southern Wisconsin. *Ecol. Monogr.* 27:351-384; 1957.

Species of breeding birds were analyzed in 64 upland hardwood stands well distributed along a gradient of vegetational differences from stands of xeric sites, dominated by black oak (*Quercus velutina* Lam.), to stands of mesic sites, dominated by sugar maple (*Acer saccharum* Marsh.).

Plant foods were most important in diets of birds in more xeric stands. Foliage-gleaners and ground-feeding insectivorous birds were most common in the more mesic stands. Tree-trunk feeders, aerial feeders, hole-nesters, and high-nesting species showed little evidence of trends along the gradient. Shrub nesters were most common in the xeric stands, and sapling nesters were most common in the intermediate and mesic stands.

Population diversity and density were greatest in the intermediate stands, because the stands are well within the ecological amplitude of many woodland birds. In spite of many species, population density was lowest in the xeric stands. Mesic stands had fewer species, but a fairly dense population. **I-C**

Bruns, H. The economic importance of birds in the forest. *Bird Study*. 7:193-208; 1960.

Birds can remove substantial proportions of insect populations when these populations are low. The proportion of an insect population removed by birds does not increase with insect irruptions. The most important effect of birds is the prevention of insect irruptions. Use of nest boxes can increase density of birds from 5 to 20 times; thus, efforts to increase densities of birds are not wasted. **Introduction, III**

Buckner, Charles H. The role of vertebrate predators in the biological control of forest insects. *Annu. Rev. Entomol.* 11:449-471; 1966.

Because birds and mammals are homoiothermic, they operate at relatively high metabolic levels and show prospects of high potential as forest insect predators. Three basic measures must be taken for a real understanding of a predator-prey system: density of prey, density of predators, and extent of destruction of prey by predators. Birds are chiefly arboreal and prey on stem, foliage, or free-flying stages of the insect pests; most mammals are fossorial and prey mainly upon ground-inhabiting stages of insects. **I-A**



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Buckner, Charles H. Avian and mammalian predators of forest insects. *Entomophaga*. 12:491-501; 1967.

Reviews the role of the predator, and states that both functional and numerical responses are important because a strong functional response may more than counterbalance a weak, negative, or random numerical response. **I-B**

Buckner, C. H. Vertebrate predators. Toward integrated control. Proceedings of the third annual northeastern forest insect work conference. USDA For. Serv. Res. Pap. NE-194. Upper Darby, PA: Northeast. For. Exp. Stn.; 1971: 21-31.

Reviews the role of vertebrates as predators of forest insects and advocates an integrated approach to forest pest control. **I-A**

Buckner, C. H.; Turnock, W. J. Avian predation on the larch sawfly, *Pristiphora erichsonii* (HTG) (Hymenoptera : Tenthredinidea). *Ecology*. 46:223-236; 1965.

Among birds collected in or near tamarack bogs, 43 of 54 species were predators of the larch sawfly. Birds feeding in the tree crowns utilized sawflies to a greater degree than birds feeding in the shrub layer or those that captured their prey in flight. Predation varied within and between taxonomic groups of birds, and important predators were found in every group collected. Warblers were less important as predators of larch sawfly than were fringillids. Many bird species preferred adult sawflies, even when they were relatively rarer than larvae. Larger and then smaller larvae followed in order of preference. Positive functional responses were indicated at low and high prey densities for 22 predators, negative for four, and no response for two. Population censuses provided data on 34 of the predator species in two plots. Numerical responses were suggested for all except those of sporadic occurrence. Nonresident species were prominent in the plot with a high prey density. Birds are likely to influence sawfly population trends at low insect densities, and perhaps at higher densities as well. **I-A**

Carolin, V. M., Jr.; Stevens, Robert E. Key to small lepidopterous larvae in opening buds and new shoots of Douglas-fir and true firs. USDA For. Serv. Res. Note RM-365. Fort Collins, CO: Rocky Mount. For. and Range Exp. Stn; 1979. 4 p.

Presents a field key for identifying lepidopterous larval associates of western spruce budworm, *Choristoneura occidentalis* Freeman. **II-C**

Cheshire, W. F. Bird populations and potential predation on the spruce budworm. 1954; Can. Dep. Agric. Sci. Serv. Annu. Tech. Rep., Green River Proj. 1953, Sect. 14.

Provides data on bird and spruce budworm populations. **I-B**

Colquhoun, M. K. The density of woodland birds determined by the sample count method. *J. Anim. Ecol.* 9:53-67; 1940.

In sampling woodlands the unit of time, not space, is preferred together with a slow observing speed and a random rather than a fixed course. A census was taken at the same time, and the figures are tabulated for comparison. A formula is given from which a coefficient of conspicuousness for each species can be obtained, and tentative coefficients are given for those species which bred within the area. **I-D**

Colquhoun, M. K.; Morley, A. The density of downland birds. *J. Anim. Ecol.* 10:35-46; 1941.

Counts of individual birds on grass downland were made in the winter, prebreeding, and breeding seasons; each series covered 26 miles in 13 hours. The distance at which each bird was identified was also recorded, and by using a "normal identification distance" for each species, an attempt was made to compute the actual density per square mile. Conspicuousness characteristics are discussed, especially in their relationship to the observed results by the sample count method. The total population per 100 acres (40 ha) was computed as 14, 35, and 32 for the three periods. **I-D**

Colquhoun, M. K.; Morley, A. Vertical zonation in woodland bird communities. *J. Anim. Ecol.* 12:75-81; 1943.

Zonal indexes were computed for common bird species in five vertical zones. The zonal index is the relative niche of occurrence in the vegetation; in the nonbreeding season, it is identical with the feeding niche. The vertical distribution and relative abundance of each species were shown diagrammatically. Each zone had its own dominant species. Three separate vertical communities existed in British oak woods: the upper canopy community, the tree and shrub community, and the ground community. Food supply was the basis of these communities. **I-C**

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Conner, R. N.; Hooper, R. G.; Crawford, H. S.; Mosby, H. S. Woodpecker nesting habitat in cut and uncut woodlands in Virginia. *J. Wildl. Manage.* 39:144-150; 1975.

In forest areas common flickers, *Colaptes auratus*, nested only in dead snags in 1- to 12-year-old clearcuts. Pileated woodpeckers, *Dryocopus pileatus*, nested in mature, dense stands with high basal area; downy woodpeckers, *Dendrocopos pubescens*, nested in sparsely stocked stands with lower basal area. The hairy woodpecker, *D. villosus*, nested in stands intermediate to and overlapping the habitats selected by the pileated and downy woodpeckers. All nest cavities of the four species of woodpeckers were excavated in decayed wood of trees infected by fungal heart rots. Timber management may be detrimental to woodpeckers if all decayed trees are removed. Uncut strips along streams and roads are valuable woodpecker nesting habitats. **III**

Coppel, Harry C.; Mertins, James W. Biological insect pest suppression. New York: Springer-Verlag; 1977. 314 p. (Advanced series in agricultural sciences 4.)

Discusses the historical, theoretical, and philosophical bases of biological insect pest suppression; organisms used in classical biological insect pest suppression (including birds); manipulation of the biological environment for insect pest suppression; and integrated pest suppression. Studies to determine the significance of birds as pest-regulating agents are reviewed, as well as European-Asian efforts to enhance bird predation of forest pests.

Efforts to determine the food preferences of birds have led to the development of (1) artificial nest materials, platforms, and boxes to attract and hold birds; (2) artificial bird nestling mimics to allow specific prey identifications; (3) neck-ringing methods on fledglings to preserve insect food intact; and (4) examination techniques for identification of regurgitated food.

Environmental manipulations for improving bird populations are also reviewed. These include provision of nesting boxes and transfer of insectivorous birds from one area to another. Attempts to settle migratory birds into new areas on a permanent basis are cited. **I-A**

Coppel, H. D.; Sloan, N. F. Avian predation, an important adjunct in the suppression of the larch casebearer and introduced pine sawfly populations in Wisconsin forests. Second Annu. Tall Timbers Fire Ecol. Conf. Proc.; 1970: 259-272.

In winter predation studies, overwintering birds caused significant loss in casebearer population. Spring predation studies using exclusion cages showed that there was significantly more predation on the uncaged trees than on the cased trees. **III**

Crawford, H. S.; Titterington, R. W. Effects of silvicultural practices on bird communities in upland spruce-fir stands. Proceedings of the workshop management of Northcentral and Northeastern forests for non-game birds. USDA For. Serv. Gen. Tech. Rep. NC-51. St. Paul, MN: North Central For. Exp. Stn.; 1979: 110-119.

Composition and density of bird populations in upland spruce-fir stands are influenced by the admixture of hardwoods with softwoods, the vertical and horizontal structure of the stand, and the extent of spruce budworm infestation of the stand. Silvicultural practices modify all three factors and influence bird populations. **I-C**

Custer, T. W.; Pitelka, F. A. Correction factors for digestion rates for prey taken by snow buntings (*Plectrophenax nivalis*). *Condor*. 77:210-212; 1975.

Analyses of stomach contents of birds are complicated by differential rates of digestion and therefore by variable bias according to diet composition. Correction factors were developed for prey items ingested by snow buntings near Barrows, Alaska. Nonstarved buntings were force-fed a variety of foods, and their stomach contents were analyzed at given time intervals. Of the invertebrates used as prey, spiders remained distinguishable the shortest time (18 min) and carabid beetles the longest time (38 min). Small seeds were recognizable for a longer time (150 min) than insects or spiders. **II-A, B**



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DeAngelis, D. L. Estimates of predator-prey limit cycles. *Bull. Math. Biol.* 37:291-299; 1975.

Perturbation methods are applied to a differential equation predator-prey model to find the approximate amplitudes and period of limit-cycle solutions. In the model, the feeding rate per unit predator per unit prey decreases as the prey becomes scarce. The rigorous applicability of the perturbation technique depends on the assumptions that the limit-cycle amplitude is relatively small and that near the equilibrium point the growth rate of each species is most sensitive to changes in the density of the other species. The second assumption usually is roughly satisfied in practice, and examples are considered that suggest that the first assumption can be greatly relaxed. IV

DeVos, A. Changes in the distribution of mammals and birds in the Great Lakes area. *For. Chron.* 39:108-113; 1962.

Fires, forest insects, and timber management have affected the distribution and abundance of some species of mammals and birds. Woodland caribou, lynx, marten, and spruce grouse were seriously affected by environmental changes; other species, however, including white-tailed deer, moose, bobcat, and ruffed and sharp-tailed grouse have benefited greatly from manmade changes in forests. Spruce budworm outbreaks have killed extensive stands of balsam fir and white spruce, thus making it possible for heavy regeneration of suitable browse species for deer and moose. I-C

Dillery, D. G. Post-mortem digestion of stomach contents in the savannah sparrow. *Auk.* 82:281; 1965.

Compares the stomach contents of 80 sparrows injected (1.0 cm<sup>3</sup> of 10 percent formalin) immediately after death with the stomach contents of 47 sparrows not injected. Injected birds contained parts of 13.8 animals per bird, whereas the noninjected birds contained parts of only 5.1 animals per bird. Various groups of prey animals are digested at different rates, both before birds are killed and also after they are killed if digestion is not stopped immediately. II-B

Dowden, Philip B.; Buchanan, W. D.; Carolin, V. M. Natural control factors affecting the spruce budworm. *J. Econ. Entomol.* 41:457-464; 1948.

Birds were credited with terminating a spruce budworm infestation in British Columbia. The 1912 outbreak in Minnesota may have been precipitated by the scarcity of small insectivorous birds, notably warblers, after severe snow and ice storms late in the springs of 1907 and 1910. I-A

Dowden, Philip B.; Carolin, V. M. Natural control factors affecting the spruce budworm in the Adirondacks during 1946-1948. *J. Econ. Entomol.* 43:774-783; 1950.

Reasons for the decline of a budworm infestation in the Adirondacks were compared to causes for continuation of the outbreak in Ontario, Quebec, New Brunswick, and northern Maine. Most important natural control factors were overwintering mortalities, parasitization by entomophagous insects, and predation by insectivorous birds. I-A

Dowden, Philip B.; Jaynes, H. A.; Carolin, V. M. The role of birds in a spruce budworm outbreak in Maine. *J. Econ. Entomol.* 46:307-312; 1953.

Typical second growth spruce-balsam areas in northern Maine were used to study the effect of insectivorous birds on a spruce budworm infestation. Stomach contents of 826 birds collected on the experimental area were examined. Among resident birds, warblers, followed by thrushes and sparrows, consumed the most budworms. Reduction in budworm population was far greater in the check areas where birds were unmolested than in areas where birds were controlled by shooting. I-A



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Eberhardt, L. L. A preliminary appraisal of line transects. *J. Wildl. Manage.* 32:82-88; 1968.

Extensive field data are needed on the frequency of sightings classified by distance from the observer's path. A classification of processes underlying transect observations shows the need for models tailored to fit each kind of sighting, because it is important to distinguish between those effects that depend on the observer's behavior and those that depend primarily on an animal's reaction to the observer's presence. **I-D**

Emlen, J. R. Population densities of birds derived from transect counts. *Auk*. 88:323-341; 1971.

Census methods for nonflocking land birds are reviewed, and a method is described that is applicable at all seasons, is more efficient than intensive plot methods, and is apparently comparable in accuracy. In the new method, foot transect counts are made and all detections, both visual and aural, are tallied to the limit of detectability. The count for each species is then multiplied by a conversion factor (coefficient of detectability) which represents the percent of the population that is normally detected by these procedures. Conversion values are derived directly from distribution curves of detection points that are lateral from the observer's trail. Conversion values are finally adjusted for incompleteness in the strip of optimum coverage close to the transect trail. Field procedures used in testing the new method are described, and samples of preliminary results are presented and evaluated. **I-D**

Emlen, J. R. Estimating breeding season bird densities from transect counts. *Auk*. 94:455-468; 1977.

Transect and plot map census methods are compared. The transect method is applicable during any season, and the plot map method can be used only during the breeding season. More area can be covered per unit of time in the transect method than in the mapping method. Problems of reliability for both methods are discussed. **I-D**

Ersine, Anthony J. Birds in boreal Canada: communities, densities and adaptations. 1977; Can. Wildl. Serv. Rep. Ser. 41. 73 p.

An overall review of the boreal avifauna, its composition, evolution, and prospects for survival. Major regions and topics include conifer forests, broad-leaved forests, forest structure and habitat partitioning, open habitats, wetland and riparian habitats, and artificial environments. Distribution patterns, community structure, seasonal distribution, and the impact of man are also discussed.

Regular and abundant members of the conifer forest avifauna are listed by forest habitat, including censuses in the presence and absence of spruce budworm. Densities of breeding birds in coniferous forests rise through a succession, from 100 to 200 pairs per km<sup>2</sup> in open jack-pine stands or low bog forests through 200 to 400 pairs per km<sup>2</sup> in spruce, to 300 to 600 pairs per km<sup>2</sup> in balsam fir. Still higher densities, over 800 pairs per km<sup>2</sup>, occur in the presence of spruce budworm outbreaks in mixed coniferous-deciduous stands. **I-B,C**

Franz, J. M. Biological control of insect pests in Europe. *Annu. Rev. Entomol.* 6:183-200; 1961.

A review of research on biological control of pest insects in Europe, including Western Russia, since 1945. Major topics are microbial control (viruses, protozoa, bacteria, and fungi); entomophagous insects; and entomophagous birds. **Introduction, III**

Franzreb, Kathleen E. A comparison of variable strip transect and spot-map methods for censusing avian populations in a mixed-coniferous forest. *Condor*. 78:260-262; 1976.

Where dense vegetation hampers detectability and results in underestimation of population size, the spot-map method is more accurate. In comparison to the spot-map method, the transect method requires less time and fewer observers to census a given amount of habitat.

**I-D**

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Gage, S. H. Consumption by adult birds of the spruce budworm at different larval densities. Fredericton, NB: For. Res. Lab., Marit. Reg.; 1968; Intern. Rep. M-36. 5 p.

Describes a study undertaken in New Brunswick to measure numbers of spruce budworm larvae consumed by forest birds at low, medium, and high budworm densities. Birds were shot, and numbers of budworm mandibles in the intestine and gizzard were counted. It was assumed that the number of birds shot over a 2-day period provided an index of bird density. Increased numbers of replications are needed to improve the reliability of the shooting method.

Even at low larval densities, budworms were an important component of the avian diet. All sampled bird species showed a marked increase in consumption as budworm populations increased from low to medium density. However, this did not hold true as populations increased from medium to high density, except for the bay-breasted warbler. Some species showed only a moderate response, whereas others showed a definite decrease in consumption. **I-A**

Gage, S. H.; Miller, C. A. A long-term bird census in spruce budworm-prone balsam fir habitats in Northwestern New Brunswick. 1978; Marit. For. Res. Cent. Inf. Rep. M-X-84. 6 p.

A long-term bird census was conducted in five plots located in largely balsam fir stands of Northwestern New Brunswick. During part of the 22-year census, two of the plots were heavily infested with spruce budworm and suffered extensive tree mortality. Nineteen bird species were common to all plots; differences in their densities, relative to forest cover and presence of budworm as a food supply, are presented. **I-C**

Gage, S. H.; Miller, C. A.; Mook, L. J. The feeding response of some forest birds to the black-headed budworm. *Can. J. Zool.* 48:359-366; 1970.

Predatory effects of nine species of forest birds on large-larval and pupal stages of black-headed budworm were investigated for 3 years on the Green River watershed in New Brunswick. Response curves show changes in consumption in relation to changes in prey size, density, and other characteristics within a season. Percentage of predation varied from 3 to 14 percent over the 3 years and strongly suggested that birds act in a density-dependent manner. **I-B; II-B**

Gates, C. E.; Marshall, W. H.; Olson, D. P. Line transect method of estimating group population densities. *Biometrics.* 24:135-145; 1968.

A new estimator is proposed for estimating ruffed grouse population densities by the line transect method of sampling. The estimator, using only the right angle distances from the observer to the sighted animal, is shown to be approximately unbiased, and an approximate variance of the estimator is provided in explicit form. Both the estimator and its variance are dependent on specified assumptions. The expected length of line transect necessary to sample exactly  $n'$  animals is derived as well as the additional miles needed to achieve a predetermined precision. The underlying assumptions are discussed and several are tested. **I-D**

George, John L.; Mitchell, Robert T. Calculations on the extent of spruce budworm control by insectivorous birds. *J. For.* 46:454-455; 1948.

During June and July 1946, studies were conducted at Lake Clear Junction, N. Y., to determine the effect of feeding spruce budworm larvae killed by DDT to nestling birds. A systematic census of insectivorous birds of the spruce-fir forest in the area was used in conjunction with estimations of the budworm population to determine degree of control. Insectivorous birds provided 3.5 to 7 percent control. **I-A**

Graham, S. A. The intersection method of counting animals. *J. Wildl. Manage.* 4:313-314; 1940.

This method is based on the principle of locating a point by intersecting lines. Drumming ruffed grouse were censused by this method. It is recommended that songbirds be censused by this method, but the census must be conducted just before sunup. **I-D**



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Graham, S. A. The apparent imbalance between birds and forest insects. *Scientia*. 102:667-668; 1967.

Describes the interactions between birds and forest insects, including spruce and jack pine budworms. Estimates of forest bird numbers and food requirements indicate that birds are unable to control pest populations once they reach outbreak proportions. Resident birds, may, however, prevent outbreaks from occurring when pest populations are low. Bird predation operates in a limited density-dependent manner. Predatory activities increase as the pest population increases until the pest exceeds food requirements of resident birds. Flocking birds moving into areas of high pest density may help check the outbreak, but the degree of control depends on size of the outbreak and available flocking birds.

Decimation of birds might also release an insect outbreak that otherwise would not have occurred. For example, severe late freezing weather during warbler migrations in southern Minnesota and Wisconsin killed numerous insectivorous birds. Two years later (1912) an outbreak of the spruce budworm began in northern Minnesota. I-A

Greenberg, Russell. Body size, breeding habitat, and winter exploitation systems in *Dendroica*. *Auk*. 96:756-766; 1979.

Large warbler species are generally restricted to breeding in coniferous forests and woodlands. Among the largest warblers are taiga breeding species and species specializing on spruce budworm outbreaks. On wintering grounds, these species often display opportunistic exploitation patterns: intraspecific mingling and unstable foraging behavior. Hypotheses are offered for the origin and evolution of coniferous-restricted species. III

Griffiths, K. J.; Holling, C. S. A competition submodel for parasites and predators. *Can. Entomol.* 10:785-818; 1969.

Presents a generalized competition model for predators or parasites developed from a specific parasite-host system. The model was structured in three parts: the first simulates the effects of exploitation, the second concerns interference between searching predators and parasites, and, the third concerns the outcome of competition between parasite progeny within their host. Percentage of predation and progeny production were affected by different degrees of contagion in the distribution of attacks, by scramble versus contest competition, and by the degree to which parasites could avoid hosts already attacked. IV

Hairston, N. G.; Smith, F. E.; Slobodkin, L. B. Community structure, population control, and competition. *Am. Nat.* 94:421-425; 1960.

The authors conclude that (1) populations of producers, consumers, and decomposers are limited by their respective resources in the classical density-dependent fashion; (2) interspecific competition must necessarily exist among the members of each of these three trophic levels; and (3) herbivores are seldom food-limited but appear most often to be predator-limited and, therefore, are not likely to compete for common resources. I-A

Hartley, P. H. T. The assessment of the food of birds. *Ibis*. 90:361-381; 1948.

Reviews the materials for investigation, sampling methods, and assessment and presentation of results for bird food studies. Qualitative knowledge of the food of many birds is fairly complete, but there is little quantitative information. Materials available for study of bird foods include examination of stomach contents, pellets, dung, rejected meals, accumulated stores, and field notes of observers and photographs. Statistically satisfactory samples of stomach contents from any one locality or habitat may be impossible.

Bird foods may be assessed by (1) frequency of occurrence, (2) enumeration, (3) weight, or (4) volume. There is no one ideal method; the food of each species or group of species should be investigated and assessed by methods that seem most appropriate. I-A, D; II-A,B,C

Hassell, M. P. Evaluation of parasite or predator responses. *J. Anim. Ecol.* 35:65-75; 1966.

Review of the terms functional response and numerical response and their weaknesses when applied to population dynamics. I-B

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Hayne, D. W. An examination of the strip census method for estimating animal populations. *J. Wildl. Manage.* 13:145-157; 1949.

The usual method of strip census assumes that flushing distances observed by the investigator constitute a good sample for all animals throughout the population studied. Since this assumption appears to be incorrect, population estimates based on observed average flushing distances are in error.

To estimate flushing distance, it is suggested that the population of each class of animal be estimated separately; the sum of these several subpopulation estimates is the estimate of total population. A formula is given for this computation.

Two previously suggested sources of error, namely, the movement of animals out of the observer's path, and the failure of the observer to sight animals flushing to the right or left, are discussed. **I-D; IV**

Hensley, M. M; Cope, J. B. Further data on removal and repopulation of breeding birds in a spruce-fir forest community. *Auk*. 68:483-493; 1951.

This study is a continuation of the field work done in 1949 near Fort Kent, Maine, by Stewart and Aldrich. **I-B**

Holling, C. S. The functional response of predators to prey density and its role in mimicry and population regulation. 1965; *Mem. Entomol. Soc. Can.* 45. 60 p.

Discusses the latest step in a systems analysis of predation. It concerns the functional response of predators to density of their prey and presents the experimental and theoretical basis for extending an earlier explanation of the response of invertebrates to include that of vertebrates. This expansion requires the addition of one new component—learning—to those components that determine the response of invertebrates; that is, rate of successful search, time predator and prey are exposed, time spent handling each prey, and hunger. The explanation of action and interaction of these components was incorporated into a mathematical model that predicts three different types of response to the density of palatable prey. In a Type 1 response, the curve showing the effect of increasing prey density on the number of prey attacked per predator per day has a linear rise to a plateau. Type 2 and 3 responses, on the other hand, have negatively accelerated and S-shaped rises, respectively, to plateau. Each of the three types of predation differs in its regulatory properties. Increasing the number of species of predators increases the chance for stable regulation of prey populations. **IV**

Holling, C. S.; Buckingham, S. A behavioral model of predator-prey functional responses. *Behav. Sci.* 21:183-195; 1976.

Describes a general simulation model of the predation process developed from an experimental analysis of the action and interaction of the basic and subsidiary components of predation. Eight qualitatively distinct classes of predation can be identified together with the biological conditions for each. With this classification it is possible to compress the complexity into a tested and analytically tractable equation of predation that has broad descriptive power. Such an equation can serve as a building block to develop ecosystem simulations whose stability properties can be explored rigorously. **IV**

Holmes, Richard T.; Schultz, John C.; Nothnagle, Philip. Bird predation on forest insects: an enclosure experiment. *Science*. 206:462-463; 1979.

Exclusion experiments showed that birds significantly reduced low-level densities of larval Lepidoptera on striped maple, *Acer pensylvanicum* L., in a deciduous forest understory. No significant differences were detected between control and experimental groups for densities of Arachnida, Coleoptera, Homoptera, and Hemiptera. Weekly removal rates of caterpillars from understory foliage by birds ranged from 18 to 63 percent and averaged 37 percent. Greatest removal coincided with nestling and fledgling periods of insectivorous birds in the forest. Bird predation may act both as a population regulator and as a strong agent of natural selection. **I-A**

Jackson, J. A. A quantitative study of the foraging ecology of downy woodpeckers. *Ecology*. 51:318-323; 1970.

Discusses intersexual partitioning of the foraging niche, seasonal variation in the relative frequency of the modes of foraging, variation in the mode of foraging on live versus dead trees, and seasonal variation in the use of live and dead trees. Partitioning of the foraging niche by the sexes is accomplished behaviorally by a differential use of the available substratum according to limb height and diameter. The degree to which these unisexual subniches are expressed varies on live versus dead trees. Both male and female downy woodpeckers use subsurface foraging techniques to a greater extent during the winter and superficial techniques during the warmer months. Greater use of dead trees during the winter is also indicated. **III**



Jackson, Jerome A. Insectivorous birds and North American forest ecosystems. James G. Dickson [and others], eds. The role of insectivorous birds in forest ecosystems. New York: Academic Press; 1979a; 1-7.

Discusses the role of insectivorous birds in natural control of forest insect pests. North American insectivorous forest birds are characterized by (1) period of feeding on insects, (2) migratory status, (3) cavity nesting, and (4) foraging site. Major insect pests of North American forests are tabulated by parts of trees attacked, their overwintering site, and developmental stage during overwintering. I-A

Jackson, Jerome A. Tree surfaces as foraging substrates for insectivorous birds. James G. Dickson [and others], eds. The role of insectivorous birds in forest ecosystems. New York: Academic Press; 1979b; 69-93.

Patterns of variability in tree surfaces are related to the suitability of surfaces as habitats for arthropods and foraging sites for insectivorous birds. Tree species and age diversity, and extent of forest environments are important factors influencing population dynamics of forest arthropods and insectivorous forest birds. Maintenance of diversity contributes to forest health by providing varied habitats and food resources for insectivorous forest birds. I-A

James, F. C. Ordinations of habitat relationships among breeding birds. *Wilson Bull.* 83:215-236; 1971.

Two methods of multivariate analysis (principal component analysis and discriminant function analysis) were applied to determine how breeding bird species distribute themselves in the structure of the vegetation. The vegetation was sampled in 0.1-acre circular plots; singing male birds were used as the center of the circles. The two statistical methods applied to the vegetational data described bird distribution along gradients of vegetational structure. I-C

Jennings, Daniel T.; Houseweart, Mark W. Sexing spruce budworm pupae. USDA For. Serv. Res. Note NE-255. Broomall, PA: Northeast. For. Exp. Stn.; 1978. 2 p.

Spruce budworm pupae can be sexed by the location and shape of the genital opening. The opening spans the eighth abdominal segment in female pupae and is found on the ninth segment in male pupae. II-C

Johannsen, O. A. Spruce bud-worm (*Tortrix fumiferana*, Clemens). 1913; *Maine Life Sci. Agric. Exp. Stn. Bull.* 210. 31 p.

Describes early outbreaks of spruce budworm, susceptible host trees, damage, life stages, and natural enemies including birds. The budworm was controlled naturally by birds including the purple martin, which was once very common in Maine. I-A

Kendeigh, S. C. Measurement of bird populations. *Ecol. Monogr.* 14:67-106; 1944.

Analyzes known methods for measuring bird populations; many methods are illustrated from original data. An analysis was made of the species composition and the population of each species in mature, relatively undisturbed climax forests at various localities within the deciduous forest biome. The total population of forest-interior species amounted to 200 pairs per 100 acres (40 ha). I-D

Kendeigh, S. C. Community selection by birds on the Helderberg Plateau of New York. *Auk.* 62:418-436; 1945a.

Community selection by birds of shrubby fields or forests rather than grassland is correlated with the use of elevated positions for songposts, nest sites, or feeding areas. Selection of forests rather than shrubby fields or grassland is correlated with the avoidance of high light intensity and with a greater restriction of free movement.

Preference for either evergreen or deciduous forest is correlated primarily with the size and shape of the leaves and with their arrangement on the twig rather than with differences in persistence of the foliage in food supply or in microclimate. This preference is effected in different species through choice of material used in nest construction, in choice of nest site, or in manner of feeding.

Avoidance or reduction of interspecific competition is an important factor in the evolutionary development of a preference for a particular niche. I-C



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Kendeigh, S. C. Nesting behavior of wood warblers. *Wilson Bull.* 57:145-164; 1945*b*.

Territory, home range, song, display, nest building, egg laying, incubation, and brooding behavior are discussed for various species of wood warblers. **III**

Kendeigh, S. Charles. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. 1947; Ont. Dep. Lands and For. Biol. Bull. 1. 100 p.

Effects of spraying DDT on birds and other wildlife were investigated on a large tract of coniferous forest in Ontario. The food habits of birds were determined by field observations of actual feeding activities and by studying stomach contents of birds. During an outbreak, it is unlikely that the birds can control the budworm.

**I-A,B**

Kendeigh, S. C. Bird populations and biotic communities in northern lower Michigan. *Ecology*. 29:101-114; 1948.

Biotic communities are best delimited by the life-form or structure of the dominant vegetation correlated with the occurrence of distinct groupings of animal species. **I-C**

Kennedy, Martin E. Assessing the role of vertebrates in the biological control of invertebrate populations. *Clyde, NC: Haywood Tech. Inst.*; 1978. 196 p.

A literature review of fish, birds, mammals, reptiles, and amphibians. Categorical listings are given by habitat of invertebrate pests and various vertebrates reported to have partially or completely controlled them. References to vertebrates preying on the spruce budworm are given and include mostly wood warblers. **I-A**

Kilham, L. Courtship and territorial behavior of hairy woodpeckers. *Auk*. 77:159-270; 1960.

A detailed study of one pair of hairy woodpeckers. Includes comparisons with other species. **III**

Kluijver, H. N. Food consumption in relation to habitat in breeding chickadees. *Auk*. 78:532-550; 1961.

Twenty-five broods were observed; special attention was given to parental feeding of the young. Data are given on clutch size, hatching success, nestling food, number of feedings per day, and disintegration of family groups. **III**

Koplin, J. R. The numerical response of woodpeckers to insect prey in a subalpine forest in Colorado. *Condor*. 71:436-438; 1969.

Woodpeckers increased in density 50 times in response to an increased population of insect prey in fire-killed trees. Aggregation, not increased reproduction, caused woodpecker increase. **III**

Koplin, J. R. Measuring predator impact of woodpeckers on spruce beetles. *J. Wildl. Manage.* 36:308-320; 1972.

A deterministic model was formulated to predict predatory impact of three species of woodpeckers on endemic, epidemic, and panepidemic populations of larval spruce beetles. The input included (1) food requirements of woodpeckers, (2) average number of prey per woodpecker stomach, (3) population density of woodpeckers, and (4) air temperature, and the output was number of prey consumed. Predictions from the model compared favorably with estimates made by measuring relative survival of larvae inside and outside woodpecker exclosures. The model predicted that northern three-toed woodpeckers were the most effective and downy woodpeckers the least effective predators of spruce beetles. It is speculated that the graded predatory effectiveness was related to foraging adaptations characteristic of each species. The combined predatory impact of the woodpeckers was least effective on endemic and panepidemic populations, and most effective on epidemic populations. It is also speculated that decreased predatory effectiveness on endemic populations is related to the availability of alternate prey and to adaptations of woodpeckers for utilizing them. And, decreased predatory effectiveness on panepidemic populations is related to numerical response limitations imposed by nesting territoriality. **IV**

Korschgen, Leroy J. Procedures for food-habits analyses. Schemnitz, Sanford D., ed. *Wildlife management techniques manual*. 4th ed. revised. Washington, DC: Wildl. Soc.; 1980:113-127.

Describes general principles, materials, methods, analytical procedures, nutrition, bioenergetics, field studies, and related activities for food-habits analyses of birds. **II-A,C**

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Lack, D. The natural regulation of animal numbers. London: Oxford Univ. Press; 1954. 343 p.

A survey and synthesis of recent research on factors limiting animal numbers, especially birds. Clutch sizes and brood numbers are governed by available food. Chapters deal with population stability, food, predation, disease, climate, cycles, mass emigration, migration, gregariousness, and dispersion. Food shortage is viewed as the most important mortality factor for most animal species. I-A

Lawrence, L. de K. Comparative study of the nesting behavior of chestnut-sided and Nashville warblers. Auk. 65:204-219; 1948.

Nesting behavior of these two species of warblers was compared. Similarities and differences in nests, clutches, incubation, behavior of young nestlings, sanitation of nests, song, and displays are discussed. III

Lawrence, L. de K. Nesting life and behavior of the red-eyed vireo. Can. Field Nat. 67:47-77; 1953.

Discusses a study of the red-eyed vireo conducted in central Ontario. Includes arrival in spring, territories, prenesting activities, nests, nest building, egg laying, incubation, care of young, development of young, defense behavior, renesting and nesting success, feeding habits, voice, and departure from nesting grounds. III

Lea, R. B. A study of the nesting habits of the cedar waxwing. Wilson Bull. 54:225-237; 1942.

The activities of 12 nests were recorded; the average incubation period for 18 marked eggs was 11.7 days. The average clutch was 4.0 eggs. The nestling stage averaged 15.5 days. The female waxwing did all the incubating and brooding. As the nestling grew, feeding rate increased and brooding time decreased. Duties of the male became more important, and the female spent less time at the nest. Fledglings apparently remained in the vicinity of the nest until they were at least 1 month old. III

Leopold, A. Game management. New York: Charles Scribner's Sons; 1933. 481 p.

Discusses mark-recapture census. I-D

MacArthur, R. Population ecology of some warblers of northeastern coniferous forests. Ecology. 39:599-619; 1958.

Cape May and, to a lesser degree, bay-breasted warblers depend on periods of overabundant food; whereas, yellow-rumped (myrtle), blackburnian, and black-throated green warblers maintain populations roughly proportional to the volume of foliage of the type in which they normally feed. Differences in feeding position, behavior, and nesting date reduce competition. These factors, combined with slight differences in habitat preference and perhaps greater intraspecific than interspecific competition, allow the species to coexist. I-B; III

MacArthur, R. H.; MacArthur, A. T. On the use of mist nets for population studies of birds. Proc. Nat. Acad. Sci. USA 71:3230-3233; 1974.

Birds captured in mist nets, marked, and released can be used to estimate size of population through a decline in capture rate. I-D

MacArthur, R. H.; MacArthur, J. W.; Preer, J. On bird species diversity. II. Predictions of bird census from habitat measurements. Am. Nat. 96:167-174; 1962.

Breeding birds can be estimated from measurements of the amounts of foliage in three horizontal layers. The abundance of each species is roughly determined by the number of patches of vegetation whose foliage profile is acceptable to that species. One habitat supports more bird species than another because it has a greater internal variation in vegetation profile—a variety of different kinds of patches. Vegetation at many heights above the ground will simultaneously support ground dwellers, shrub dwellers, and canopy dwellers. I-C

MacKay, M. R. The larvae of *Choristoneura fumiferana* (Clem.) and *C. pinus* Free. (Lepidoptera: Tortricidae). Can. Entomol. 85:128-133; 1953.

Describes the second- and last-instar larvae of spruce budworm and the last-instar larva of jack pine budworm. Characteristics for distinguishing larvae of the two species are discussed. II-C



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Manly, B. F. J.; Miller, P.; Cook, L. M. Analysis of a selective predation experiment. *Am. Nat.* 106:719-736; 1972.

A new index of selection,  $\alpha$ , measures the degree to which a predator is more likely to take one kind of prey rather than another, and thus provides a direct estimation of predator behavior. The index is unaffected by sampling in a finite population, which is an advantage over other methods of estimating selectivity.

If selection is independent of the frequency of prey types,  $\alpha$  is constant. Under frequency-dependent predation,  $\alpha$  changes with frequency. Measures of the frequency-independent and the frequency-dependent components may be obtained when both kinds of selection act together. IV

Marten, G. G. An optimization equation for predation. *Ecology*. 54:92-101; 1973.

A general equation is derived for the quantity of different foods a predator consumes in response to food preference and food abundance. Presumably the predator apportions its efforts among different search modes in order to minimize the discrepancy between actual and desired quantities of each food consumed. Included are the conflict between quantity and composition of the diet and the competition between feeding and non-feeding activities. IV

Martin, N.D. An analysis of bird populations in relation to forest succession in Algonquin Provincial Park, Ontario. *Ecology*. 41:126-140; 1960.

Censuses of breeding birds were taken in most of the major forest types during the breeding seasons of 1952 and 1953. The approximate areas of the bird territories were measured, and the vertical depth of territories was determined by recording heights above the ground at which birds were observed. Vertical dimensions of territories were small compared to horizontal dimensions; consequently, territory volume varied chiefly in proportion to area. Most birds nested near the bottoms of territories, had songposts near the tops of territories, and consumed insect larvae from the tree foliage or trunks.

Total bird populations per 100 acres (40 ha) were 286 territorial males of 13 species in bog, 232 territorial males of 32 species in boreal forest, 279 territorial males of 28 species in *Tsuga* forest, and 168 territorial males of 18 species in hardwood forest. I-C

Mattson, William J. Negligible feeding responses by birds to variations in abundance of the budworm *Choristoneura pinus* (Lepidoptera: Tortricidae). *Great Lakes Entomol.* 7:104-112; 1974.

Budworm consumption was at a peak even at low levels of infestation, and birds exerted cybernetic pressure on budworm numbers only at endemic levels. I-A

Mattson, W. J.; Knight, F. B.; Allen, D. C.; Foltz, J. L. Vertebrate predation on the jack pine budworm in Michigan. *J. Econ. Entomol.* 61:229-234; 1968.

Twenty-eight species of birds and one mammal attacked the jack pine budworm in Michigan. Birds were more important than mammals as budworm predators. I-B

May, R. M. Limit cycles in predator-prey communities. *Science*. 177:900-902; 1972.

Essentially all models proposed for predator-prey systems have either a stable point equilibrium or a stable limit cycle. This stable limit cycle, an explicitly non-linear feature, is commonly overlooked in conventional analyses of these models. Such a stable limit cycle provides a satisfying explanation for those animal communities in which populations oscillate. IV

Mendall, H. L. Nesting of the bay-breasted warbler. *Auk*. 54:429-439; 1937.

Nesting of the bay-breasted warbler was observed from June 12 to July 12, 1936, in South Thomaston, Maine. Descriptions of the nest, incubation, hatching, feeding of young, and disturbance of the nestlings are related. III

Miller, C. A. A key to some lepidopterous larvae associated with the spruce budworm. *Can. Dep. Agric. For. Insect Invest. Bi-Mon. Prog. Rep.* 6:1; 1950.

Contains a field key for distinguishing spruce budworm larvae from allied species found feeding on spruce-fir foliage. II-C



Mitchell, Robert T. Consumption of spruce budworms by birds in a Maine spruce-fir forest. *J. For.* 50:387-389; 1952.

An experiment was conducted near Fort Kent, Maine, to determine the effectiveness of birds in controlling outbreaks of spruce budworm. Stomach contents in birds were identified, and budworm volume was estimated. Actual numbers of budworms were too difficult to ascertain. On the basis of stomach analyses and feeding pressure values, warblers appeared to be outstanding among birds in reducing the spruce budworm populations. Thrushes and sparrows were next in importance. I-A

Mook, L. J. Birds and the spruce budworm. Morris, R. F., ed. *The dynamics of epidemic spruce budworm populations.* Mem. Entomol. Soc. Can. 31:268-271; 1963.

To assess the influence of birds on the survival of the spruce budworm, it is necessary to know the functional response to prey and predator densities; the numerical response of the predator; the influence of the composition and numbers of the alternate food complex; and the attractiveness of the study area for birds compared with that of surrounding areas. Bird predation is greatest during the sixth-larval instar and during the pupal stage. I-A,B

Mook, L. J.; Marshall, H. G. W. Digestion of spruce budworm larvae and pupae in the olive-backed thrush, *Hyloichia ustulata swainsoni* (Tschudi). *Can. Entomol.* 97:1144-1149; 1965.

Mandibles and cremasters were used for identification of spruce budworm remains in bird gizzards in studies at the Green River Watershed, New Brunswick. These structures are heavily sclerotized and can be identified long after the soft parts have become unrecognizable. In the olive-backed thrush, soft parts and sclerotized parts of pupae are digested at different rates, and about 75 percent of the number ingested will be retained during the 2-hour period before the bird dies. I-A; II-B,C

Morris, R. F. Predation and the spruce budworm. Morris, R. F., ed. *The dynamics of epidemic spruce budworm populations.* Mem. Entomol. Soc. Can. 31:244-248; 1963.

Predation by arthropods, birds, and small mammals is considered. Wood warblers probably do not prey on eggs, but they do prey on pupae. Gizzards analyses indicate that very few larvae smaller than the fifth instar are taken by birds. It is only in the large-larval period that the relation between survival and population density suggests that predators play an important role at low population densities.

Birds prey on other insects besides the spruce budworm, and to understand their interactions with the budworm it is important to know the quantity and palatability of the alternative foods available each year on the foliage. For example, another defoliating insect, the black-headed budworm, *Acleris variana* (Fern.), reached a high population level in the late 1940's. This may have relieved predation pressure on the spruce budworm and thus aided population release.

The budworm is available to terrestrial mammals only when populations are high and the loss of foliage causes many larvae to drop from the trees. Under these conditions, mice and shrews feed readily on budworm larvae, but this represents only one of the subsidiary effects of overpopulation. The deer mouse, *Peromyscus maniculatus abietorum* Bangs., is partially arboreal and has been trapped without difficulty in the crowns of mature fir trees in Green River stands. Woodpeckers and red squirrels have also been observed feeding on larvae. I-A

Morris, R. F.; Cheshire, W. F.; Miller, C. A.; Mott, D. G. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. *Ecol.* 39:487-494; 1958.

The population trend of each species of predator was compared to the population trend of the spruce budworm during the 10-year period of census. A direct numerical response was shown for some birds; whereas, other birds showed an inverse response. Populations of rodents and insectivores showed no response but fluctuated independently of budworm density. I-B; III

Morse, D. H. Competitive relationships between parula warblers and other species during the breeding season. *Auk*. 84: 490-502; 1967a.

Parula warblers inhabited edges of spruce forests in Maine, and in Louisiana they were uniformly throughout an oak-gum forest. Most foraging was on tips of foliage where the birds' low weight appeared advantageous. **III**

Morse, D. H. The contexts of songs in black-throated green and blackburnian warblers. *Wilson Bull.* 79:64-74; 1967b.

In a climax spruce forest in Maine, blackburnian warblers foraged higher than other warbler species, with black-throated green warblers directly below. Magnolia and yellow-rumped (myrtle) warblers foraged at lower levels. **III**

Morse, D. H. A quantitative study of foraging male and female spruce-woods warblers. *Ecology*. 49:779-784; 1968.

Males of each species foraged at a greater average height than females. Males foraged nearer to the height of singing perches than to the height of nests, and principal females foraged nearer to the nests than to the singing perches of the males. **III**

Morse, D. H. Ecological aspects of some mixed-species foraging flocks of birds. *Ecol. Monogr.* 40:119-168; 1970.

Flocks of chickadees, titmice, woodpeckers, nut-hatches, creepers, kinglets, and wood warblers were studied in several habitats in Louisiana, Maryland, and Maine. Both the size of the flock and density of birds varied with the habitat. **III**

Morse, D. H. The foraging of warblers isolated on small islands. *Ecology*. 52:216-228; 1971.

Parula, yellow-rumped (myrtle), and black-throated green warblers were studied on seven small spruce-clad islands off the coast of Maine. Each island supported one pair of one to three of these species. Data obtained were compared with earlier studies of these species in large adjacent populations. When only one species was present, it was always the parula warbler; when two species were present, they were always the parula and yellow-rumped (myrtle). Black-throated green warblers were present only when the latter two species were present. Parula and yellow-rumped (myrtle) warblers

experienced greater nesting success than black-throated green warblers. Black-throated green warblers foraged much as they did in large populations; however, yellow-rumped (myrtle) and parula warblers demonstrated considerably more plasticity in foraging. When black-throated green warblers were absent, the two other species tended to modify their foraging. On the one island studied in detail when only parula warblers were present, they appeared to expand their foraging range farther than when yellow-rumped (myrtle) warblers were present. Black-throated green warblers dominate the other two species socially, and the implications of this situation upon distributions in large populations and on small islands are discussed. **III**

Morse, D. H. The foraging of small populations of yellow warblers and American redstarts. *Ecology*. 54:346-355; 1973.

On several small islands off the coast of Maine, yellow warblers and redstarts partition their habitats laterally and lack a well-marked interspecific social hierarchy, whereas spruce-woods warblers partition their habitats vertically and have a well-defined interspecific social hierarchy. Thus, only the yellow warbler or the redstart is expected to be found in a space too small to allow establishment of two distinct lateral territories. By contrast, as many as three species of spruce-woods warblers are found on small islands that usually would support only a pair of any one species. Both groups of species appear to be responding to the usual situations experienced in large mainland populations. **III**

Morse, D. H. Variables affecting the density and territory size of breeding spruce-woods warblers. *Ecology*. 57:290-301; 1976.

Species with dense populations had small territories, and the reverse was also true. Territory size usually fluctuated even less than population density, although some territories eventually increased markedly after strong declines in abundance. Warblers took lepidopteran larvae in preference to other prey. The number of warbler species in an area was closely related to the physical characteristics of the forest, but interactions among these species mediated many of the differences in density or species composition. **I-C**



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Morse, D. H. Populations of Bay-breasted and Cape May warblers during an outbreak of the spruce budworm. *Wilson Bull.* 90:404-413; 1978.

Foraging patterns, food supplies, and population densities of Bay-breasted and Cape May warblers were studied during a spruce budworm outbreak in spruce-fir forests of northern Maine. Bay-breasted warblers concentrated their foraging activities at medium to medium-low heights on dead limbs and on inner and peripheral parts of live limbs. In contrast, Cape May warblers concentrated their activities on peripheral parts of foliage near tops of trees. Both species foraged more frequently on red spruces than on other trees.

Bay-breasted warblers were common on both coniferous and mixed coniferous-deciduous census plots. Cape May warblers were much less common than Bay-breasted warblers and were found primarily in low-lying areas with tall red spruces and balsam firs. Other insectivorous birds occupied both study sites.

On the basis of seasonal consumption rates, budworm populations/ha and budworms removed/ha by birds are estimated. Budworm numbers far exceeded food demands of these warblers and other insectivorous birds. Estimated percentage of total budworms removed by birds ranged from 1.0 to 2.6 for the coniferous site; 2.5 to 6.3 for the coniferous-deciduous site. I-A, III

Nicholson, A. J. The balance of animal populations. *J. Anim. Ecol.* 2:132-178; 1933.

Animal populations are generally in a state of balance. The observed relation between fluctuations of the physical environment and fluctuations in population densities is inexplicable except in terms of balance. Competition appears to be the only factor capable of producing balance in populations, and among animals the most important competition is that which occurs when searching for things required for existence. Such competition is expressed by a single formula (and curve) of general application. For each species there is a

particular population density, referred to as the steady density, at which balance may exist; competition tends to cause populations to reach and to maintain their respective steady densities.

When populations are controlled by competition for food or suitable places to live, their densities progressively approach their steady values. When they are controlled by natural enemies, however, an oscillation (interspecific oscillation) in density about the steady value is produced, even in a constant environment. In certain situations, successive oscillations increase in amplitude, and ultimately lead to a state in which the animals are present in widely scattered groups, whose positions continually change. In other situations, successive oscillations decrease in amplitude, and ultimately cause the steady densities to be reached and maintained in a constant environment. I-A

Nicholson, A. J. An outline of the dynamics of animal populations. *Aust. J. Zool.* 2:9-65; 1954.

Influences that affect population densities and population systems are discussed. Animal population data are analyzed and systematized. Populations are self-governing systems, and regulate their densities in relation to their own properties and those of their environments. I-A

Oaten, Allan; Murdoch, William W. Functional response and stability in predator-prey systems. *Am. Nat.* 109:289-298; 1975a.

Two measures of stabilization by a functional response are proposed. Predation may be regarded as stabilizing at a prey density of  $H$  if the predation rate is increasing, that is, if  $f(H)/H$  is increasing where  $f$  is the functional response. This is the same as assuming that an increase in prey density results in an increased chance of a given prey being killed by the predator. With  $H_m$  as the maximum value of  $H$  for which this criterion holds, the measures used are  $H_m$  and  $f(H_m)$ . This criterion and these measures are related to local stability, structural stability in a modified Lotka-Volterra model, and a general multispecies model. The criteria can be used in detailed models of switching in predators and of patchiness. I-A,B; IV



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Oaten, Allan; Murdoch, William W. Switching, functional response, and stability in predator-prey systems. *Am. Nat.* 109:299-318; 1975*b*.

A model of the functional response of a predator feeding on two species of prey is considered. It is assumed that the predator searches randomly at constant speed for randomly distributed prey; but whether it attacks a contacted prey will depend on the species of the prey, the species of the last meal, and the time since the last meal. If it is assumed that the probability of attack is independent of time, it is possible to obtain a fairly simple expression for functional response. This functional response is not necessarily stabilizing; it will be if there is a sufficiently strong (relative to the handling times) tendency for the predator to attack a contacted prey, if the prey is the species that was eaten last. Relative attack rates are considered. First take the ratio of the two functional responses (for species 1 and 2), and next regard the sequence of meals as a Markov chain. The relative attack rate is a function only of relative density, and switching occurs only if the product of the probabilities of attacking the same species as last eaten is greater than the product of the probabilities of attacking the other species. It is possible to have switching and yet not have a stabilizing functional response. I-A,B; IV

Odum, E. P. Annual cycle of the black-capped chickadee—1. *Auk*. 58:314-333; 1941*a*.

The chickadee population varied considerably throughout the year with peaks in the fall and winter. Courtship and mating took place before the establishment of a definite nesting territory. Little evidence was found for the existence of definite pairs in winter flocks, though pairs remained together after nesting. The breakup of winter flocks was gradual with pairs or single birds separating out a few at a time. Courtship is apparently simple though prolonged. Establishment and defense of a definite nesting territory begin about the time of cavity excavation and end when the young leave the nest. III

Odum, E. P. Annual cycle of the black-capped chickadee—2. *Auk*. 58:518-535; 1941*b*.

Both male and female chickadees work together in excavating the nesting cavity, though the female apparently takes the lead. Size and lining materials of nests are described as well as clutch size. No evidence was found that the male incubates. The behavior of the adults is described during incubation and after hatching. Nestlings remain in the nest 16 to 17 days and remain with their parents only 3 to 4 weeks. The juveniles scatter widely in late summer whereas adults tend to remain on or near their former territories. III

Odum, E. P. Annual cycle of the black-capped chickadee—3. *Auk*. 59:499-531; 1942.

Vocal activity is very important in regulating the behavior of chickadees, especially during the flocking period. The characteristic autumn and winter flocks are rather loose aggregations of seven to eight individuals with no defined leaders. Warblers, vireos, and ruby-crowned kinglets consistently flock with chickadees during late summer and fall. Roosting, feeding, and flock movements are discussed. Winter feeding ranges averaged 36 acres. III

Otvos, Imre S. The effects of insectivorous bird activities in forest ecosystems: an evaluation. Dickson, James G. [and others], eds. *The role of insectivorous birds in forest ecosystems*. New York: Academic Press; 1979: 341-374.

Insectivorous birds have significant effects on the population dynamics of many forest insects including bark beetles and defoliators, such as spruce and jack pine budworms. The greatest effect is exerted at endemic population levels. Birds suppress and delay pest population buildup and increase the interval between insect outbreaks. Insectivorous birds may also accelerate the decline of a pest outbreak.

Indirect effects include predation on parasites and predators of the target pest species, dispersal of entomogenous pathogens, and alteration of prey microhabitat. Other roles of birds in forest ecosystems include dispersal of seeds of various forest trees and shrubs, and dispersal of wood rotting fungi. I-A

Ouellet, H. Further observations on the food and predatory habits of the gray jay. *Can. J. Zool.* 48:327-330; 1970.

The gray jay has been observed feeding on a variety of items ranging from animal carcasses to axle grease and dried fruits. The predation of gray jay on nests and young of several species of birds and on certain small mammals in the coniferous forest was also observed.

This bird may be an important predator and scavenger.

III

Outram, I. Morphology and histology of the reproductive system of the male spruce budworm, *Choristoneura fumiferana*. *Can. Entomol.* 102:404-414; 1970.

The morphology and histology of the internal reproductive system of the male spruce budworm moth are described and discussed. II-C

Outram, I. Morphology and histology of the reproductive system of the female spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Can. Entomol.* 103:32-34; 1971.

The morphology and histology of the internal reproductive system of the female spruce budworm moth are described and discussed with notes on spermatophore and egg development. II-C

Palmer, R. S. Maine birds. 1949; Harvard Univ. Mus. Comp. Zool. Bull. 102. 656 p.

A historical review of bird life in Maine. Data are given by species and include number, seasonal occurrence, migration, breeding, and general ecology. III

Pitelka, F. A. Breeding behavior of the black-throated green warbler. *Wilson Bull.* 52:3-18; 1940.

In northern Michigan the black-throated green warbler is found chiefly in developmental communities where conifers grow in pure or mixed stands. Phases of the breeding cycle have the following time periods: nest building, 4 days; incubation, 12 days; nestling life, 8 to 10 days; and dependent period of fledglings, about 4 weeks. Nests are placed at various heights in conifers. Materials used in nest structure apparently vary according to availability. Both sexes (but chiefly the female) participate in nest building and care of the young. Observations at 3- and 5-day stages of nestling life indicate that feeding increases during the nestling period, and brooding decreases and apparently ends on the seventh day. III

Pyke, G. H.; Pulliam, H. R.; Charnov, E. L. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* 52:137-154; 1977.

Reviews the mathematical models used to predict the foraging behavior of animals. The situations to which optimal foraging theory has been applied can be divided into four categories: (1) choice of food to eat, (2) choice of patch type to feed in, (3) optimal allocation of time to different patches, and (4) optimal patterns and speed of movement. Each category is discussed, as well as future developments in optimal foraging theory. The models now being used will require modification. IV

Ramsden, David J.; Lyon, L. Jack; Halvorson, Gary L. Small bird populations and feeding habitats—western Montana in July. *Am. Birds* 33:11-16; 1979.

Avian densities were determined on seven uncut forest units, four clearcuts, and one burned area in a montane forest of western Montana in July 1976. Bird populations were inventoried by survey line techniques, and vegetation was sampled by estimating percent of foliage cover within six vertical intervals.

A total of 1,116 small birds, belonging to 38 species, was recorded. Average population densities ranged from 89 to 263 individuals/km<sup>2</sup> for study units. No single unit had as many as 20 species; one unit had as few as 10. Overall averages for the 12 units were 14.0 species, 165 individuals/km<sup>2</sup>, and a mean biomass of 38.4 g/ha. Data grouping by clearcut-uncut-burn, habitat, and aspect showed few significant deviations in average number of species, densities, and biomass. Correlations were found between feeding guilds and community plant structure. Foliage-insect feeders were observed most often in uncut forest types. I-C

Rapport, D. J. An optimizing model of food selection. *Am. Nat.* 105:575-587; 1971.

An optimization model has been developed for the analysis of food selection behavior. Based on predator preferences and prey availability, the model determines the numbers and types of prey species consumed. Preferences are expressed as an ordinal ranking of all possible prey combinations. The model generates hypotheses concerning conditions for predator switching and other predator strategies. IV



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Robbins, C. S. Recommendations for an international standard for a mapping method in bird census work. Audubon Field Notes 24:723-726; 1970.

Proposes standards for bird census by the mapping method. I-D

Robbins, J. D.; Rain, A. Late winter movements and social behavior of the black-capped chickadee. Jack-Pine Warbler 48:66-72; 1970.

Individual ranges of black-capped chickadees varied from about 5 to 80 acres. An open field within the range decreased the food supply per unit area and caused the chickadees to forage over larger areas. Flocks averaged 3.3 birds. Flocks seemed to exist only where the ranges of individual birds overlapped. III

Rogers, D. Random search and insect population models. J. Anim. Ecol. 41:369-383; 1972.

Equations are discussed and developed to describe parasite search for a host. There is some discussion concerning the application of these equations to predation in general. There is a difference between the success of random search by parasites and predators that depends on handling time. Only when handling time is negligible is it possible to predict the success of search. When handling time is appreciable, two different equations must be used. It may be possible to model nonrandom parasite and predator search by assuming that it consists of a series of random searches carried out for different periods of time. IV

Rosenzweig, M. L.; MacArthur, R. H. Graphic representation and stability conditions of predator-prey interactions. Am. Nat. 97:209-222; 1963.

The general nature of the predator-prey interaction is depicted as a graph of predator versus prey densities. Conditions for stability of the interaction are predicted from this graph. An example of a three-species interaction is also presented. Variations of the graph show that an otherwise unstable interaction may be stabilized by the presence of either an inviolable prey hiding place, or extremely low predation pressure at moderate predator and high prey densities, or another predator-limiting resource. Stability is always conferred when the predator is severely limited at its equilibrium density by one of its resources other than supply of prey. Predators tend to be limited at equilibrium densities by more than one of their resources. When either of the two foregoing situations occurs, regular predator-prey oscillations

should not be observable. The stability of the interaction close to equilibrium was found to depend exclusively, in the mathematically-continuous model, on the slopes of two lines in the graph at equilibrium. Stability can be asymptotic rather than oscillatory. An equation for the period of oscillatory interactions is also advanced. The effects of natural selection on the isoclines, and thus the stability, is not clear cut. Selection of the prey tends to stabilize the interaction; the opposite is true for selection on the predator. IV

Royama, T. Factors governing the hunting behavior and food selection of the great tit (*Parus major* (L.)). J. Anim. Ecol. 39:619-668; 1970.

Discusses the underlying mechanisms of the hunting behavior and selection of prey species by great tits feeding their young at the nest. Factors governing the utilization of prey species are highly complicated. There seems to be no direct correlation between prey biomass and the tits' selection. The occurrence of many lepidopterous species in the nestlings' diet coincided with their time of pupation and suggest that the behavior of the prey has some importance in relation to predation. Effects of taste and conspicuousness of the prey species and of alternative prey occupying different microhabitats are discussed.

With the aid of a theoretical model, Tinbergen's theory of search images is critically reviewed and an alternative theory proposed. The model is based on one fundamental assumption that the predator tries constantly to maximize its hunting efficiency.

The concept of profitability, defined as the amount of food that the predator can collect for a given amount of hunting effort, is introduced into the model. The relationship between profitability and density of a given prey species is investigated. Profitability of a prey species is determined not only by the density but also by the size of the prey and the method of hunting of the predator. The size of prey has some bearing on the selection of food by tits and influences differences in the composition between the diets of adults, fledglings, and nestlings. IV



Royama, T. A comparative study of models for predation and parasitism. 1971; Res. Popul. Ecol. 13. Suppl. 1. 91 p.

The basic structure of predation and parasitism is presented in terms of mathematical equations of general forms. Two different sets of inferences are discussed—one leading to a model for predation and the other to a model for parasitism.

The logical structure in classical models (those proposed before 1935) is sound, but the assumptions involved are often inadequate to describe an actual biological system; recent models (proposed after 1955) either involve contradiction in logic or are much too often erroneously applied to the analysis of actual predation and parasitism. IV

Royama, T. Population persistence and density dependence. Ecol. Monogr. 47:1-35; 1977.

Reformulates the notion of density dependence and shows how this notion plays an important role in constructing appropriate models for data analysis. IV

Sanders, C. J. Populations of breeding birds in the spruce-fir forests of northwestern Ontario. Can. Field-Nat. 84:131-135; 1970.

Breeding populations of birds in the spruce-fir forests of northwestern Ontario during a low population density of the eastern spruce budworm averaged 123 pairs/100 acres (40 ha) compared with 319 observed by Kendeigh. The difference can be attributed to the virtual absence of four species of warblers that are known to respond numerically to increases in budworm density. I-B

Seierstad, S.; Seierstad, A.; Myrsetrud, I. Statistical treatment of the inconspicuousness problem in animal population surveys. Nature. 206:22-23; 1965.

Describes a statistical method for estimating population survey efficiency. The method is based on the assumption that a given population may be counted several times and that it is possible to determine whether an individual revealed during one count is also discovered on other counts. The number of such rediscoveries indicates the effectiveness of the census and is used to arrive at an estimate of total population. Survey efficiency expresses the probability of discovering an individual in the population (called the discovery-chance) during a count. The estimator proposed for the discovery-chance is  $\hat{p} = X_{pc}/X_c$  where  $X_c$  is the number of checks and  $X_{pc}$  is the number of positive checks. I-D; IV

Shaub, M. S. Eastern evening grosbeak summer records. Bird-Banding 27:157-165; 1956.

Summer observations of evening grosbeaks in New Brunswick, New York, and New England during 1954 and 1955 are reported. At the Green River Laboratory in New Brunswick, it was noted that there was a sudden increase in the breeding numbers of evening grosbeaks in areas under spruce budworm attack. I-B

Simmons, Gary A.; Sloan, Norman F. Consumption of jack-pine budworm, *Choristoneura pinus* Freeman, by the eastern chipping sparrow, *Spizella passerina* (Beckstein). Can. J. Zool. 52:817-821; 1974.

A method of estimating predation of birds on a forest insect is offered as an alternative to standard methods employing insect pest surveys, singing-male counts, and gizzard analyses. In this study in northern Michigan, singing-male counts and bird-banding records provided estimates of bird populations. Budworm consumption rates were estimated from observation cages. Budworm populations were estimated from branch sample counts. Average rate of consumption of all life forms of the budworm was 7.8 per hour per bird and remained nearly the same regardless of the number of life stages of the budworm available. I-A

Sloan, N. F.; Simmons, G. A. Foraging behavior of the chipping sparrow in response to high populations of jack pine budworm. Am. Midl. Nat. 90:210-215; 1973.

Discusses the foraging behavior of the chipping sparrow on high population levels of jack pine budworm. Cage studies indicated that the chipping sparrow can recognize parasitized larvae and pupae and avoid them. The "specific search image" of Tinbergen was demonstrated. I-A

Solomon, M. E. The natural control of animal populations. J. Anim. Ecol. 18:1-35; 1949.

Control of a population is a result of the limited capacity of the ecosystem for that species or for its enemies, or both. The limiting influence begins to operate at densities far below the capacity limit and intensifies as this limit is approached. An enemy is density-dependent in its action on a host (or prey) population if

it attacks a greater proportion as the host density increases. The presence of competitor species, and sometimes that of alternate hosts or prey, affects the action of the control factors involved. Four phases of control are distinguished: limitation, which sets a variable upper limit; conservation, which tends to prevent extreme reduction; suppression, or a forced decline from high density; and release, a temporary escape from normal control after a severe reduction. Each is effected by characteristic density relationships. Suppression and release promote fluctuations. The level of abundance depends ultimately on all major elements of the ecosystem, though the density-related controlling factors are the immediate determinants. **I-A**

Stefanski, R. Utilization of the breeding territory in the black-capped chickadee. *Condor*. 69:259-267; 1967.

The selected areas of the prenesting stage gradually changed into territories in the classical sense. The original territory boundaries were disregarded by the birds during the fledgling stage. Average territory sizes of prenesting and nest-building stages were 2.2 and 2.3 ha, respectively. During the most critical stage (while feeding nestlings) the birds utilized only 22 percent of the area originally established in the nest-building stage. **III**

Stenger, J. Food habits and available food in ovenbirds in relation to territory size. *Auk*. 75:335-346; 1958.

Food availability is related to ovenbird territory size. The weight of invertebrate food on the forest floor increased during the breeding season to reach a peak during the first 2 weeks of July, which corresponded with the nestling period of the ovenbird chicks. There is some evidence that lepidopterous larvae may be a preferred food. **III**

Stevenson, James. Experiments on the digestion of food by birds. *Wilson Bull.* 45:155-167; 1933.

Experiments on food digestion by small passerine birds include (1) time of feeding and holding capacity of the stomach; (2) length of small intestine and variation with sex, age, and type of food consumed; (3) rate of food passage through digestive tract; (4) amount of food consumed daily; (5) percentage of food digested; (6) environmental effects on rate of feeding; and (7) survival time of birds without food. The rate of food passage was about the same for birds fed insects, fruit, or grain; that is, the first voided excrement appeared in about 1.5 hours after ingestion of dyed foods. **II-B**

Stewart, R. E.; Aldrich, J. W. Breeding bird populations in the spruce region of the Central Appalachians. *Ecology*. 30:75-82; 1949.

The Maine coast and central Appalachian areas together represent a phase of the northern coniferous forest region that is quite different ecologically from that characteristic of western Ontario. The difference is possibly accentuated by an unusual outbreak of insects in the latter region. **I-C**

Stewart, Robert E., Aldrich, John W. Removal and re-population of breeding birds in a spruce-fir forest community. *Auk*. 68:471-482; 1951.

The effective control of breeding birds during a spruce budworm infestation was explored. In the experimental area, an attempt was made to eliminate or drastically reduce the bird population by use of firearms, whereas in the control area the natural bird population was unmolested. Some species showed a supersaturated population of males. This high population indicated that the carrying capacity of the area, as far as breeding territory was concerned, was insufficient. The spruce budworm infestation could possibly have accounted for this supersaturation. **I-B**

Stewart, R. E.; Aldrich, J. W. Ecological studies of breeding bird populations in northern Maine. *Ecology*. 33:266-268; 1952.

Breeding bird censuses were run in different forest biotic communities: boreal spruce-fir, scrub black spruce bog, alder bog shrub, white cedar/tamarack/black ash bog, yellow birch/beech/sugar maple, aspen, field border and wood margin, agricultural field and sedge meadow, lakes and streams, and miscellaneous habitats. Species compositions in the various habitats were comparable to similar associations in Ontario and western Maine. Populations were probably inflated because of an abundance of spruce budworm prey. **I-B**

Sturkie, Paul D. *Avian physiology*. 2d ed. Ithaca, NY: Comstock Publ. Assoc.; 1965. 766 p.

A text on avian physiology devoted especially to the physiology of the chicken, the duck, and the pigeon. Major topics include the nervous, circulatory, digestive, excretory, and reproductive systems; regulation of body temperature; energy metabolism and metabolism of carbohydrates, proteins, and lipids; and thyroids, parathyroids, adrenals, and pancreas. An extensive bibliography is included. **II-B**



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Swanson, G. A.; Bartonek, J. C. Bias associated with food analysis in gizzards of blue-winged teal. *J. Wildl. Manage.* 34:730-746; 1970.

The food contents of 67 adult and flying juvenile blue-winged teal collected during the spring and summer months of 1967 and 1968 on prairie wetlands in central North Dakota were statistically compared. The result was disagreement in food composition between the esophageal and gizzard contents. Differences observed in wild birds were confirmed experimentally in 13 feeding trials in which drake blue-winged teal were fed natural foods and then killed at time intervals ranging from 2.5 minutes to 72 hours later. The magnitude of the bias related to digestibility increased in direct proportion to the time lapse between feeding and sampling. Soft foods broke down within minutes whereas hard seeds were retained for days. Reliable information can be obtained by analyzing esophageal contents, by collecting birds that are actively feeding and immediately removing contents of the esophagus, and by preserving foods in 80 percent alcohol. **II-A,B**

Tinbergen, L. Dynamics of insect and bird populations in pine woods. *Arch. Neerl. Zool.* 13:259-472; 1960.

Presents factors determining the food of tits in pine-woods during spring and summer. The percentage of food formed by an individual prey species was determined by season, density, and size and palatability of prey. The risk of predation for a new prey species in the environment is low at first and increases suddenly and then decreases. A hypothesis was formed that tits, when searching for prey, concentrate on one or a few species at a time; and learn to develop a specific searching image for these species. The difference in risk between low and moderate densities is explained by assuming that the birds do not adopt a specific searching image for a species of prey that is scarce. Risk decreases at high densities when the prey species form more than a critical percentage in total food. **III**

Titterton, R. W.; Crawford, H. S.; Burgason, B. N. Songbird responses to commercial clearcutting in Maine spruce-fir forests. *J. Wildl. Manage.* 43:602-609; 1979.

In commercially clearcut and uncut spruce-fir (*Picea* spp., *Abies* sp.) stands of northern Maine, the distribution of breeding songbirds was determined by habitat structure. The authors grouped 14 sampling areas into five seral stages: stage I—dense slash and open ground; stage II—dense raspberry stems, and deciduous woody stems less than 2 m tall; stage III—deciduous woody stems 2.1 to 4.5 m tall; stage IV—deciduous woody stems taller than 4.5 m and trees with d.b.h. 10 to 15 cm; and stage V—a dense softwood overstory. Presence or absence of a softwood overstory was the most important habitat feature. Each seral stage was dominated by a characteristic group of breeding bird species. The data showed a predictable pattern in response of the breeding avifauna to changes in habitat structure after clearcutting. **I-C**

Tothill, John D. Notes on the outbreaks of spruce budworm, forest tent caterpillar, and larch sawfly in New Brunswick. *Proc. Acadian Entomol. Soc.* 8:172-182; 1923.

In New Brunswick, where budworm had escaped suppressive predation, a higher percentage of budworm was killed by death of the host tree than any other individual factor. In British Columbia, under more heterogeneous forest conditions, the greatest percentage of budworm was killed because of avian predation. **I-C**

Van Tyne, Josselyn. An unusual flight of Arctic three-toed woodpeckers. *Auk.* 43:469-474; 1926.

Reports the abundance and movement of black-backed (Arctic) three-toed woodpeckers after the 1909 to 1914 outbreak of spruce budworm in Eastern Canada and Maine. Woodpecker populations apparently increased because of the abundance of wood-boring insects attacking recently killed timber. **I-B**



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Watt, K. E. F. A mathematical model for the effect of densities of attacked and attacking species on the number attacked. *Can. Entomol.* 91:129-144; 1959.

The assumptions underlying five classical mathematical models of host-parasite and predator-prey population dynamics are inadequate to account for published data. A new model has been developed and tested against available data. Methods of obtaining parameter values for the model from field and laboratory data are outlined and illustrated. **IV**

West, G. C.; DeWolfe, B. B. Population energetics of taiga birds near Fairbanks, Alaska. *Auk*. 91:757-775; 1974.

The birds in two adjacent areas of taiga in interior Alaska were censused from late May to the end of August by a modification of the trail census method. The population and estimated energy removal increased in July and decreased again in August. In general, the increase in July was a result of production of young; the decrease in August was a result of death and emigration from the census area. There were fewer breeding birds and their biomass on the two sites censused than those reported in other localities within the boreal forest from Northwest Territories, southern Ontario, or northern Minnesota. **I-D**

Williams, A. B. The composition and dynamics of a beech-maple climax community. *Ecol. Monogr.* 6:317-408; 1936.

For a 3-year period, the average number of breeding pairs per acre was 2.3. Includes notes on population and territory. For example, a red-eyed vireo nest found in the canopy and one directly below near the ground represents a distinct vertical overlap. **I-D**

Williamson, K. Birds and modern forestry. *Bird Study* 17:167-176; 1970.

Density and species diversity of summer birds were high in young conifer plantations surrounded by a landscape fringe of mature deciduous trees. These attributes were also high where island refuges of deciduous trees and scrub were allowed to remain after clearcutting and replanting with conifers. The author maintains that the same principle can be profitably employed to diversify habitat and enrich bird life of extensive forests of Sitka spruce and other exotic conifers. **Introduction, III**

Zach, Reto; Falls, J. Bruce. Response of the ovenbird (*Aves: Parulidae*) to an outbreak of the spruce budworm. *Can. J. Zool.* 53:1669-1672; 1975.

Reports response of the ovenbirds to an outbreak of the spruce budworm in Algonquin Park, Ontario. Ovenbirds exhibited a functional response involving an unusual method of foraging. The numerical response was based on smaller, more tightly packed territories, and probably on larger first and subsequent clutches. It is suggested that the great variability in clutch size of certain wood warblers may indicate a tendency to lay successive clutches when food is abundant. **I-B; III**

Ziswiler, Vinzenz; Farner, Donald S. Digestion and the digestive system. Farner, D. S.; King, J. R., eds. *Avian biology*. New York: Academic Press; 1972: 343-430. (v. 2).

A detailed treatise on bird digestion. Review of structure and function of the digestive system: buccal cavity, buccal glands, pharynx, esophagus, crop, gastric apparatus (glandular, muscular, and pyloric stomach), intestines, cloaca, liver, and pancreas. **II-A**

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# Appendix—Scientific Names of Birds Mentioned in this Paper

Blue-winged teal	<i>Anas discors</i> L.	Red-breasted nuthatch	<i>Sitta canadensis</i> L.
Spruce grouse	<i>Canachites canadensis</i> (L.)	Robin	<i>Turdus migratorius</i> L.
Ruffed grouse	<i>Bonasa umbellus</i> (L.)	Swainson's thrush (for- merly olive-backed thrush)	<i>Catharus ustulatus</i> (Nuttall)
Sharp-tailed grouse	<i>Pedioecetes phasianellus</i> (L.)	Ruby-crowned kinglet	<i>Regulus calendula</i> (L.)
Japanese quail	<i>Coturnix coturnix japonica</i> Tem. and Schl.	Cedar waxwing	<i>Bombycilla cedrorum</i> Vieillot
Common flicker (formerly yellow-shafted flicker)	<i>Colaptes auratus</i> (L.)	Red-eyed vireo	<i>Vireo olivaceus</i> (L.)
Pileated woodpecker	<i>Dryocopus pileatus</i> (L.)	Tennessee warbler	<i>Vermivora peregrina</i> (Wilson)
Hairy woodpecker	<i>Picoides villosus</i> (L.)	Nashville warbler	<i>Vermivora ruficapilla</i> (Wilson)
Downy woodpecker	<i>Picoides pubescens</i> (L.)	Parula warbler (now Northern Parula)	<i>Parula americana</i> (L.)
Black-backed three-toed woodpecker	<i>Picoides arcticus</i> (Swainson)	Yellow warbler	<i>Dendroica petechia</i> (L.)
Northern three-toed woodpecker	<i>Picoides tridactylus</i> (L.)	Magnolia warbler	<i>Dendroica magnolia</i> (Wilson)
Hammond's flycatcher	<i>Empidonax hammondii</i> (Xántus)	Cape May warbler	<i>Dendroica tigrina</i> (Gmelin)
Western flycatcher	<i>Empidonax difficilis</i> Baird	Yellow-rumped warbler (formerly Myrtle warbler)	<i>Dendroica coronata</i> (L.)
Western wood pewee	<i>Contopus sordidulus</i> Sclater	Black-throated green warbler	<i>Dendroica virens</i> (Gmelin)
Gray jay	<i>Perisoreus canadensis</i> (L.)	Blackburnian warbler	<i>Dendroica fusca</i> (Müller)
Black-capped chickadee	<i>Parus atricapillus</i> L.	Chestnut-sided warbler	<i>Dendroica pensylvanica</i> (L.)
Boreal chickadee	<i>Parus hudsonicus</i> Forster	Bay-breasted warbler	<i>Dendroica castanea</i> (Wilson)
Great tit	<i>Parus major</i> L.	Ovenbird	<i>Seiurus aurocapillus</i> (L.)
		American redstart	<i>Setophaga ruticilla</i> (L.)
		Evening grosbeak	<i>Hesperiphona vespertina</i> (Cooper)
		Savannah sparrow	<i>Passerculus sandwichensis</i> (Gmelin)
		Chipping sparrow	<i>Spizella passerina</i> (Bechstein)
		White-throated sparrow	<i>Zonotrichia albicollis</i> (Gmelin)
		Snow bunting	<i>Plectrophenax nivalis</i> (L.)

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Relationships of birds and spruce budworms—literature  
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The relationships between birds and spruce budworms are reviewed. Literature summaries and annotated references are presented under four topic areas: (1) predation and bird populations, (2) determining consumption of budworms by birds, (3) life histories of important predaceous birds, and (4) predator-prey models. This bibliography is intended to aid those interested in investigating the relationships of forest birds and spruce budworms.

**KEYWORDS:** Birds, spruce budworm, predation, life  
histories, predator-prey models,  
*Choristoneura* spp.



